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THE EFFECT OF MANGANESE COMPOUNDS ON SOILS AND PLANTS

E. P. DEATRICK

ITHACA, NEW YORK
PUBLISHED BY THE UNIVERSITY

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E. P. Deatrick

Experimental evidence has shown that phosphorus, sulfur, potassium, calcium, magnesium, iron, carbon, hydrogen, oxygen, and nitrogen are essential to the normal growth and development of plants. Other elements, including manganese, are almost universally found in soils and plants, and this fact has led some investigators to assume that they perform important physiological functions. The weight of evidence, however, seems to indicate that the benefit following applications of a manganese compound to soil is due to its stimulative, indirect action either on the plant or on the soil, and manganese is therefore usually designated as a *catalytic fertilizer*.

The investigation here recorded was undertaken for the purpose of acquiring information regarding the specific effect of manganese compounds in increasing plant growth; in other words, to determine whether manganese is a direct plant stimulant, whether it increases the available food supply in the soil, or whether both these factors are operative. The direct stimulative or deleterious effect of a substance on plant growth may be determined by growing the plant to be studied in water cultures of a pure nutrient solution. When the same kind of plant is grown in soil to which the substance to be studied is added, the effect is usually very much modified. In the soil culture the action must be considered as the sum of the effects directly and indirectly on soil and plant.

REVIEW OF LITERATURE

Experiments with water cultures

The effects of manganese on plants have been studied by growing seedlings in distilled water alone, and in distilled water to which nutrient salts were added.

Working with the distilled water cultures, investigators have observed both stimulative and toxic effects. Loew and Sawa (1902–03)[1] found that in the presence of manganese in toxic quantities the leaves lose their

[1]Dates in parenthesis refer to *Literature cited*, page 399.

turgor and dry up, and no trace of new rootlets is apparent. In a solution containing 1000 parts per million of manganese sulfate, the leaves of barley plants faded to yellow and then turned brown. These investigators found also that barley became chlorotic and the roots turned brown in solutions containing only small quantities of manganese. McCool (1913) noted that a solution containing 15 parts per million of manganese in the form of chloride is injurious to field peas, and that a solution containing 30 parts per million prevents root growth entirely. Miss Brenchley (1914) found that manganese when present in strong concentrations exerts a toxic influence on higher plants.

On the other hand, several investigators have obtained plant stimulation in distilled water cultures containing small quantities of manganese. Micheels and De Heen (1906) obtained a pronounced stimulation in colloidal solutions of manganese. McCallum (1909) reported an acceleration of tuber formation when potatoes were treated with a solution of manganese chloride. Montemartini (1911), altho finding marked differences in the sensitiveness of plants, obtained increased growth with all plants used in his experiment. McCool (1913) found slight stimulation, as shown by length of the roots of pea seedlings, but the leaves showed no effect.

The effects of manganese in solutions containing nutrient salts are similar to those obtained with distilled water cultures, but experiments show that the nutrients greatly reduce the toxicity of the manganese. McCool (1913) found that this reduction of toxicity is proportional to the concentration of the nutrient salts.

According to Miss Brenchley (1914),

> the Rothamsted experiments supported Aso's work on the action of manganese sulphate on barley, concentrations of the salt above 1/100,000 having a retarding influence on the growth, the roots being coloured brown and the leaves also showing discolouration. At an early stage in growth the lower leaves of the plants receiving the most poison began to be flecked with brown spots.

A solution containing 1350 parts per million of nutrient salts and 770 parts per million of manganese in the form of sulfate, reduced the yield 31 per cent. A solution containing but 0.01 of this amount of manganese developed brown roots after four weeks and reduced the yield 3 per cent.

In lower concentrations manganese was decidedly stimulative. Aso (1902–03) found that manganese stimulated the growth of a number of plants. The solutions which he used contained 0.5 per cent of nutrient

salts and 0.02 per cent of manganese sulfate in one series, and 0.05 per cent of nutrient salts and 0.002 per cent of manganese sulfate in the other series.

Tottingham and Beck (1916) reported increased yields of wheat grown in nutrient solutions containing small quantities of manganese chloride.

Various views are held regarding the cause of the stimulation on the one hand and of the toxicity on the other. Loew and Sawa (1902–03) suggest that the stimulation by manganese is related to the oxidation of toxic substances within the plant leaf. They assert that certain noxious by-products are formed in the leaf, and that in reality sunlight retards growth. They state: "It is in the absence of light that growth proceeds and the products of the sun's work are chiefly consumed." Protoplasm oxidizes the carbohydrates formed, while the noxious by-products, probably members of the benzene group, are oxidized by enzymes, whose action is increased by the presence of manganese.

Many investigators find that the action of enzymes is in some way related to the presence of manganese. Kastle (1910) writes at length on manganese in its relation to the oxidizing ferments. It has been shown by Bertrand, he states, that the oxidizing power of laccase (from lucerne) is associated with the manganese content. He regards this element as the co-ferment, or activator, of laccase, just as hydrochloric acid is the co-ferment of pepsin. The oxidation of organic compounds, such as hydroquinon, by the oxygen of the air, is accelerated by the presence of manganese and varies with the form of the salt, being greater with the salts of the organic acids. These salts are "most easily hydrolyzable"; thus,

$$R''Mn + HOH = R''H_2 + MnO.$$

The manganous oxide formed is "spontaneously oxidizable." In this oxidation, "molecular oxygen is split into two atoms, one of which combines with the manganous oxide to form the peroxide, the other going to oxidize the hydroquinon"; thus,

$$MnO + O_2 = MnO_2 + O, \text{ and}$$
$$C_6H_4\,(OH)_2 + O = C_6H_4O_2 + HOH.$$

In the presence of an acid, $R''H_2$ is unstable and is capable of oxidizing more hydroquinon. Thus the manganese salt is regenerated. "According to this conception the manganese would be the really active element

of the oxidase, so far as the activation and transfer of oxygen is concerned, whereas the acid albuminoid radicle would impart to the ferment its other properties, such as its conduct toward heat, solubility, etc."

Manganese has been found to activate animal ferments. Considerable work has been done on the oxidizing power of colloidal solutions of manganese, which are described by Kastle as *artificial ferments.*

The reports of numerous investigators indicate that a relation exists between the presence of manganese and the production of chlorophyll. Van Dam (1907) states that seeds soaked in a solution of manganese sulfate yield plants which develop greener leaves than normally. Jadin and Astruc (1912) report that manganese constantly occurs in the ash of plants and that the chlorophyll-bearing parts contain the greatest proportion of this element. Mameli (1912) found that chlorophyll is produced in some of the lower plants only when manganese is added to the nutrient media. Pugliese (1913) states that there is an optimum ratio for iron and manganese, which he gives as 1:2.5. Mazé (1914) has described a special type of chlorosis due to the lack of manganese; a large amount in the plant also causes chlorosis. Gile (1916) is of the opinion that " manganese chlorosis may be due in part to a deficiency of iron in the plant, induced by the action of manganese in the plant or in the soil, and in part to a direct toxic action of the manganese." Johnson (1917) finds that the toxic effect of manganese on pineapples appears to be " due to a depression in the assimilation of iron," and has worked out a commercially successful method of counteracting the toxic effect by supplying iron thru the leaves.

Experiments with soil cultures

A large number of experiments are reported in which manganese salts have been applied to soil as a fertilizer. The results are somewhat contradictory.

Von Feilitzen (1907) found that manganese sulfate did not increase the yield of oats perceptibly. Pfeiffer and Blanck (1912), after experimenting with various salts and plants, decided that their results were not conclusive. They state that, while increased yields were occasionally obtained, the salts of manganese should not be recommended for general use as a fertilizer. This opinion is held also by Sullivan and Robinson (1913), who advised that manganese should not be used " in any way

other than in experimentation and as a fertilizer complementary to the usual chemical fertilizers." Masoni (1916) experimented with several manganese salts. Altho the chloride and the sulfate seemed to give a certain advantage, he believed the results were too small to indicate definitely the specific effect on the growth of the plants tested. Ehrenberg and Schultze (1917) state that experiments covering several years show that under many sorts of conditions neither a favoring nor an inhibitory action of manganese compounds on the growth of plants is demonstrable. At the Woburn station, however, Voelcker (1904) observed that manganese iodide, applied at the rate of 50 pounds to the acre, was very toxic to the growth of barley.

On the other hand, some surprising results have been obtained from the use of manganese salts. Javillier (1908) states that comparatively small quantities of this element have been sufficient to increase the yields of certain crops from 25 to 50 per cent. He believes there is no doubt that manganese compounds, particularly the sulfate, may be used advantageously as a complementary manure. Loew and Honda (1904–05) report an increase of 50 per cent in *Cryptomeria japonica* from fertilizing with manganese sulfate. With the use of the same salt Ray and Pradier (1909) were able to increase the yield of apricots 23 per cent. Bartmann (1910) cites Marre as having secured an increase of 60 per cent in some crops. Numerous other investigators have reported data indicating that manganese is a fertilizer of decided value.

A number of investigators, including Nagaoka (1906–08), and Skinner and his co-workers (1914, 1916), report data which are apparently contradictory. Nagaoka (1906–08) reported that in 1902 manganese sulfate applied at the rate of 70 pounds to the acre, increased the yield of rice 37 per cent; the following year the residual effect was considerable; in 1904 the season was "exceptionally favorable," but the treated plats again surpassed the checks; in 1905 the experiment was repeated, but that year the yield was greatly decreased. Skinner and Sullivan (1914) reported their work on the action of manganese in soils; they found that the growth of wheat was increased when various salts were added to a soil described as an *unproductive sandy loam,* while on a *productive loam* the salts had no stimulating effect.

Further experiments were reported by Skinner and Reid (1916), who state that "in a six-years field test of manganese sulphate used at the

rate of 50 pounds per acre on an acid silty clay loam, its effect each year was not beneficial to the crops grown." During the following years of experimentation the yields of the crops were increased. The soil had been found to be very acid, and large quantities of calcium carbonate were applied.

It appears that the reaction of the soil is a determining factor in the action of manganese. Nagaoka (1906–08) notes that the soil increases in acidity with the continued application of manganese sulfate. Rousset (1909) cites Malpeaux as securing contradictory results with both the sulfate and the chloride of manganese, but favorable results with the carbonate and the oxide applied in combination with marl.

Some results have been obtained, however, which point to a decreased stimulation when manganese is applied with some form of calcium. According to Uchiyama (1907), " A manurial mixture of a nearly neutral reaction, exerts the best effect. Manures of decisive alkaline or acidic nature on the other hand are not so favorable, since the former interferes with the effect of the manganese salt, while the latter are not suitable for the growth of most plants." Chittenden (1915–16) observed the same effect; he states that in two out of three cases manganese sulfate alone increased the yield, while the addition of lime to the manganese sulfate decreased the yield.

Many of the apparently inconsistent reports are explainable when complete data regarding the experiment are available. Some of the applications are too low. Others, as that of Crochetelle (1913), who applied an excessive amount (2000 pounds to the acre) of manganese sulfate to a " calcareous clay," are high yet stimulative.

References to the change which manganese compounds may undergo when added to soils are numerous. Nottin (1912) found that manganese is adsorbed like potassium or ammonia, and is precipitated by calcium carbonate and organic matter; the demanganization of water by calcium carbonate, and the precipitation of manganese found in dolomitized limestones, indicate that, in alkaline soils at least, the soluble salts of manganese are changed to oxides. In the soil solution, manganese probably occurs in the form of the bicarbonate, as Vincent (1916) concludes. Regarding solubility, Masoni (1916) states that the organic acids are particularly active in dissolving manganese. He claims that the behavior of the carbonates, sulfates, and oxides of manganese may be explained as phenomena of hydrolysis and of successive oxidation and reduction.

According to Schreiner, Sullivan, and Reid (1910:37), " soils may have practically the same amount of manganese and still vary greatly in oxidizing power, so oxidation in soils, if due to manganese, depends on the nature of the manganese as much as on the amount." The salts of manganese added to soils which were low in this element and had " very little oxidizing power," did not increase their power to oxidize aloin. Experiments to learn the effect on oxidation of the addition of hydroxy acids and salts to manganese compounds in the soil, led these authors to state (page 56 of reference cited): "This oxidation appears to be mainly nonenzymotic, the result of interaction between inorganic constituents and certain types of organic matter. It may also be brought about by organic matter in a state of autoxidation and by inorganic oxygen carriers, such as manganese and iron. Both processes activate oxygen."

According to Sullivan and Reid (1912:28), " That the catalytic power of the soil is correlated to some degree with the manganese content of the soil is evident." A comparison of soils of varying manganese content, and the failure of the addition of manganese salts to increase the catalytic power of soils that were poor catalyzers even tho the content of manganese was high, led these investigators to state that factors other than the " total amount of manganese must be the determinants." They suggest that either the nature of the manganese compound or the nature of the associated organic matter is more important than the amount of manganese.

Experiments with soil fungi and bacteria

Altho the experimentation is meager, the weight of evidence supports the conclusions of Bertrand (1909) that manganese stimulates the growth of fungi. Loew and Sawa (1902–03), however, found no stimulation, and they have written at length on the difference of the behavior of manganese on the growth of phanerogams.

Kelley (1912) concluded that nitrification took place more rapidly in the soil high in manganese, while ammonification was about equal in soils of either high or low manganese content. Leoncini (1910) and Montanari (1914) have found that manganese increases the activity of nitrifying bacteria.

Brown (Brown and Minges, 1916) applied various salts of manganese to soil cultures, and concluded from his data that " if manganese salts in small quantities increase crop yields on a soil, that increase may be

due in part at least to a beneficial effect on ammonification and nitrification." If, on the other hand, the salts "restrict crop growth, that restriction may be due in part to a depression of bacterial activity."

Greaves (1916) has recently published his results. He states that with the possible exception of the chloride, all the manganese salts tested were strong stimulants to the ammonifying organisms of the soil. At maximum stimulation, 25 per cent more ammonia accumulated than in the normal soil.

Olaru (1915) states that the nitrogen-fixing power of bacteria from legumes is greatly increased by manganese. Gregario (1916) finds that mannitol bouillon containing 60 parts per million of manganese in the form of the chloride and inoculated with *Bacillus radicicola* fixes three times as much nitrogen as do the checks; a concentration of 200 parts per million retards the fixation. Furthermore, he finds that *Clostridium pasteurianum*, which normally is not a free fixer, becomes capable of fixing nitrogen in the presence of manganese. Similar results have been obtained with *Azotobacter chroococcum.*

Summary

Much of the evidence in the foregoing reports is contradictory. The results would be more intelligible if complete data regarding the experiments were given. The applications of manganese salts to soils have been made without any apparent consideration of the type of soil. Such factors as soil type, the presence of calcium, and the crop to be grown, are factors that determine the action of a given application. Large applications on a sandy loam are detrimental, while the same applications on a clay loam or on a soil high in calcium would in all probability be stimulative.

The rôle of calcium seems to be a complex one. If the manganese were stimulative in the soluble form, the addition of calcium would precipitate the manganese and prevent the stimulation. If, on the other hand, the manganese were present in such concentration as to be toxic, the addition of calcium would be beneficial, not only by causing precipitation of the manganese but also by increasing the oxidizing power of the soil by such precipitation.

Altho the evidence is in many respects inconclusive, the following statements seem to be justified by this review:

1. Manganese is universally distributed in small quantities in soils and plants.

2. The majority of experiments indicate that, as Miss Brenchley (1914) states, "manganese exerts a toxic influence upon the higher plants, if it is presented in high concentration, but, in the absence of great excess of the manganese compounds, the poisoning effect is overshadowed by a definite stimulation."

3. The toxicity of manganese is reduced by nutrient solutions and by soil.

4. Manganese compounds have been associated with the catalytic power of soils and with the oxidizing power of soils and plants. Comparatively large yields have been obtained with manganese fertilization under neutral or alkaline soil conditions, and the yields have been correlated with the oxidizing power of the soil. The stimulation of plants has in part been explained as due to increased activity in the metabolic processes within the leaf.

5. A stimulation of the ammonification and nitrification in soils has also been reported.

EXPERIMENTAL WORK

Scope of present study

In order to test the effect of manganese salts on the growth of plants, the weight of wheat seedlings grown in manganese solutions of varying concentrations (both in the presence and in the absence of nutrient salts) was compared with the weight of plants grown in cultures containing no manganese. The concentrations producing stimulation were then used as a basis for the applications in the experimental work conducted to test the manurial value of manganese when applied to soils. Dunkirk silt loam was treated with various manganese salts and planted with wheat. An attempt to explain the results obtained led to a study of the oxidizing, ammonifying, and nitrifying powers of soils treated with salts of manganese.

Effect of manganese compounds on wheat seedlings grown in water cultures

Wheat seedlings (Jones' Paris Prize 106–43) from seeds germinated in running tap water were allowed to attain a growth of about eight centimeters, and were then transferred to culture containers. These were salt-mouth bottles of a capacity of 250 cubic centimeters, fitted with four-holed corks and wrapped in black paper. Each series was set up

in quadruple and was run for a period of two or four weeks. The nutrient solutions were made up from the following formulae:

Salt 1. Calcium nitrate........................	27 grams
Salt 2. Magnesium sulfate......................	6 grams
Salt 3. Potassium phosphate (monobasic).....	15 grams
Salt 4. Ferric sulfate..........................	0.5 gram
Salt 5. Potassium chloride......................	7.5 grams

Salts 1 and 5 were dissolved together in 3 liters of water; salt 2 was dissolved in 1½ liters, as was also salt 4, and both of these were mixed with salts 1 and 5. To the mixture was then added salt 3, after it had been dissolved in 3 liters of water. The total quantity was then increased to 10 liters by adding 1 liter of water. This solution contains 4656 parts per million of salts.

The wheat seedlings were placed in cultures containing 10, 20, 100, 200, 400, and 1000 parts per million of manganese in the form of manganese sulfate, and were harvested after remaining in the greenhouse for four weeks. The results are given in table 1:

TABLE 1. WHEAT SEEDLINGS (ENDOSPERMS NOT REMOVED) GROWN IN SOLUTIONS OF MANGANESE SULFATE. NO NUTRIENTS PRESENT

Parts per million of manganese	Length (in centimeters)		Weight of four plants (in grams)		Total dry weight	Relative weights
	Leaves	Roots	Leaves	Roots		
0	11.7	18.2	.0784	.0514	.1298	100
10	10.6	10.3	.0940	.0460	.1400	108
20	11.5	5.6	.0967	.0319	.1286	99
100	10.6	4.2	.0658	.0211	.0869	67
200	12.4	4.6	.0873	.0163	.1036	80
400	10.9	3.7	.0770	.0222	.0992	76
1000	9.8	3.8	.0641	.0171	.0812	63

As shown in table 1, solutions of manganese sulfate containing no nutrients were found to be toxic. All the manganese cultures, at the termination of the experiment, might be characterized as dead or dying. There was no great increase in growth, if any increase at all, even in the lowest concentration. The total dry matter was reduced in all cases except with a concentration of ten parts per million. The first symptom of the toxicity of manganese is the yellowing of the tips of the lower leaves.

Then bleaching occurs in small patches, which redden, dry, and turn brown. The intensity of this chlorotic condition decreases with the decrease in the concentration of the manganese. The roots of the plants grown in concentrations of 1000 parts per million turned brown in spots, especially at the tips, within four days. This browning occurred on the roots of all the plants except the checks, the length of time before the browning appeared being proportional to the concentration of the manganese.

The toxic effect was not so great in cultures of manganese sulfate containing nutrient salts (4656 parts per million) as in pure solutions, as is shown in table 2:

TABLE 2. MANGANESE SULFATE ADDED TO NUTRIENT SOLUTIONS CONTAINING 4656 PARTS PER MILLION OF NUTRIENT SALTS

Parts per million of manganese	Length (in centimeters)		Weight of four plants (in grams)		Total dry weight	Relative weights
	Leaves	Roots	Leaves	Roots		
0	19.4	12.0	1713	.0742	.2455	100
10	17.8	15.4	.2951	.2033	.4984	203
20	19.2	15.6	.2668	.1781	.4449	181
100	21.2	14.0	.2383	.1294	.3677	150
200	20.5	12.8	.2250	.1052	.3302	135
400	20.7	9.3	.2020	.0780	.2800	114
1000	16.0	5.9	.1581	.0459	.2040	83

This demonstrates the ameliorating effect of the nutrient salts in overcoming or reducing the toxicity of a plant poison. At 1000 parts per million the total dry matter was reduced, but it equaled the check at 400 parts per million and increased with a decrease in the concentration of the manganese. The yellowing of the tips of the leaves at 1000 parts per million commenced in nine days. The browning of the roots was not observed in any of the cultures except those of greatest manganese content.

A second series of cultures was run in which the chloride, the carbonate, and the dioxide of manganese were used in addition to the sulfate. The seedlings of the first series, reported as having grown in solutions containing no nutrient salts, were in reality not grown in the absence of other elements. That the effect of the storage food in the endosperms is a factor in work of this nature, is suggested by McCool (1913), who states:

Pea seedlings [cotyledons not removed] that have been grown for ten days in distilled water, tap water, and full nutrient solution, respectively, are much more resistant to the

poisonous influence of manganese than those that are transferred from germinating pans and placed immediately in solutions of manganese. The nature of the medium used in this preliminary treatment — that is, whether distilled water, tap water, or full nutrient solution — has no visible effect on the resisting power of the plants."

The seeds in this second series, consequently, were germinated as before, but when the seedlings were about eight centimeters high the endosperms were pinched off. This was done to eliminate as much as possible the influence of the storage food. The concentration of the nutrient solution was but one-fifth of that used in the previous series of cultures.

The average dry weight of the wheat seedlings at the time of setting up the cultures was determined, so that the effect of the manganese solutions might be the more accurately ascertained. The results are given in tables 3 and 4:

TABLE 3. WHEAT SEEDLINGS (ENDOSPERMS REMOVED) GROWN IN SOLUTIONS OF MANGANESE SALTS. NO NUTRIENTS PRESENT

Parts per million of manganese	Average dry weight (grams)	Increase or decrease in weight during the two weeks (grams)	Relative increase or decrease in weights
0	.0319	.0025	100
Manganese sulfate			
1	.0336	.0042	168
5	.0304	.0010	40
10	.0298	.0004	16
100	.0309	.0015	60
1000	.0258	—.0036	—144
Manganese chloride			
1	.0352	.0058	232
5	.0342	.0048	192
10	.0332	.0038	152
100	.0309	.0015	60
1000	.0252	—.0042	—168
Manganese carbonate			
1	.0322	.0028	112
5	.0350	.0056	224
10	.0297	.0003	12
100	.0349	.0055	220

TABLE 4. MANGANESE SALTS ADDED TO NUTRIENT SOLUTIONS CONTAINING 961 PARTS PER MILLION OF NUTRIENT SALTS

Parts per million of manganese	Average dry weight (grams)	Increase in weight during the two weeks (grams)	Relative increase in weights
0	0367	.0073	100
Manganese sulfate			
1	.0392	.0098	134
5	.0404	.0110	151
10	.0423	.0129	177
100	.0400	.0106	145
1000	.0368	.0066	90
Manganese chloride			
1	.0385	.0091	125
5	.0419	.0125	171
10	.0395	.0101	138
100	.0387	.0093	127
1000	.0320	.0026	36
Manganese carbonate			
1	.0367	.0073	100
5	.0376	.0082	112
10	.0387	.0093	127
50	.0455	.0161	220

It will be noticed that by this procedure it has been possible to show an actual decrease in the weight of the seedlings grown in the solutions of highest concentrations of the sulfate and the chloride.

An examination of tables 3 and 4, giving the results of this series of experiments, shows that these results agree in general with those of the first series; that is, as the concentration of the manganese decreases, the total dry weight increases. The figures show clearly the greater toxic effect of the manganese in the absence of the endosperm. The results here reported agree closely with those of Miss Brenchley (1914).

Effect of manganese compounds on wheat grown in soil

The determination of the effect of a given factor when added to the soil is complex. The effect of this factor on the growth of plants is but

an indication of its resultant effect on the various activities in a complex medium. It was therefore deemed advisable to determine, in the first place, whether the addition of manganese sulfate to soil cultures inhibits its power to function as in the case of water cultures. Consequently, wheat was grown on soil to which manganese sulfate had been added in varying amounts.

In this, as well as in other soil experiments, the soil used was Dunkirk silt loam, obtained near the experimental plats of Caldwell Field. The results of the chemical and mechanical analyses are given in tables 5 and 6, respectively:

TABLE 5. CHEMICAL (BULK) ANALYSIS OF DUNKIRK SILT LOAM

Constituent determined	Surface 1 to 12 inches (per cent)	Subsoil 12 to 24 inches (per cent)
Nitrogen (N)	0.186	0.082
Organic carbon (C)	1.670	0.440
Carbon dioxide (CO_2)	Trace	0.260
Calcium oxide (CaO)	0.430	0.830
Magnesium oxide (MgO)	0.450	0.690
Potassium oxide (K_2O)	1.740	2.110
Sodium oxide (Na_2O)	1.090	1.280
Phosphoric anhydride (P_2O_5)	0.123	0.126
Manganese oxide (Mn_3O_4)	0	0

TABLE 6. MECHANICAL ANALYSIS OF DUNKIRK SILT LOAM

	Per cent
Fine gravel	0.5
Coarse sand	0.8
Medium sand	0.6
Fine sand	2.7
Very fine sand	9.5
Silt	67.3
Clay	18.6

The soil was procured in quantity, was allowed to partially dry out in the air, and was then passed thru a 2-millimeter sieve. After treatment with manganese sulfate the soil was placed in small wire baskets, 350

grams to a basket. The baskets were paraffined and a sand mulch was placed on the surface. Six baskets of each treatment were set up, four of which were planted with wheat seedlings about 10 centimeters high. There were four seedlings in each basket. The baskets were carried to the greenhouse, where they remained for a period of three months. During that period they received such applications of distilled water, from time to time, as would bring the soil up to the original moisture content of 25 per cent (dry basis). On May 3, 1916, the crop was harvested, and the plants were dried, weighed, and analyzed for manganese. The results are given in table 7:

TABLE 7. WHEAT GROWN FOR THREE MONTHS ON DUNKIRK SILT LOAM TREATED WITH MANGANESE SULFATE

Parts per million of manganese added	Average weight of seedlings in each culture (grams)	Relative weights
0	2.70	100
10	3.25	120
50	2.80	104
100	1.94	72
1000	2.05	76

An examination of the relative weights shows that the manganese is at least not prevented entirely from stimulating plant growth when it is added to soil. The stimulation at 10 parts per million was appreciable.

Another set of cultures was arranged on December 12, 1916. Two kilograms of air-dry soil, to which the various quantities of manganese sulfate were added, was placed in wire baskets. These baskets then received a coating of paraffin and a sand mulch. Seven of the baskets received an application of calcium carbonate at the rate of 20,000 parts of CaO per million of soil. The soil was seeded to wheat and the moisture content was raised to 25 per cent (dry basis), where it was kept by the addition of distilled water from time to time. One month later the seedlings were thinned to five to a basket, and these were allowed to grow for seven and

one-half months. The crop was harvested on July 3, 1917. The yields obtained are recorded in tables 8 and 9:

TABLE 8. WHEAT GROWN FOR SEVEN AND ONE-HALF MONTHS ON DUNKIRK SILT LOAM TREATED WITH MANGANESE SULFATE

Parts per million of manganese added	Weight of straw		Weight of grain	
	Average (grams)	Relative	Average (grams)	Relative
0	5.6	100	2.0	100
10	5.0	89	4.0	200
25	5.7	102	4.1	205
50	3.5	62	2.3	115

TABLE 9. WHEAT GROWN FOR SEVEN AND ONE-HALF MONTHS ON DUNKIRK SILT LOAM TREATED WITH MANGANESE SULFATE AND 20,000 PARTS PER MILLION OF CALCIUM CARBONATE

Parts per million of manganese added	Weight of straw		Weight of grain	
	Average (grams)	Relative	Average (grams)	Relative
0	1.7	100	1.7	100
10	4.5	265	2.0	118
25	4.9	288	1.8	106
50	5.0	294	2.1	123

The effect of the manganese in these cultures is not apparent when the yields are considered. Practically all the yields of the soil treated with manganese are somewhat higher than those treated with calcium. The yield for the calcium carbonate check is strikingly low, for which no reason can be assigned by the writer. Greater differences, however, than those that appear in the data of table 9, were noted at an earlier stage of growth. It was observed that a majority of the manganese plants headed before the calcium-manganese plants did. In this respect it would seem that the calcium had interfered with the action of the manganese.

Other investigators have stated that the effect of manganese on yield is not marked. While Bertrand (1909) notes that the favorable results of manganese are not apparent until harvest time, Miss Brenchley (1914) states that there is a retarding effect on the ripening of the grain but not on the yield. Takeuchi (1909–13) reports that the control plants of flax were behind the manganese plants in growth and flowering. Aso (1904–05) found that rice treated with manganese flowered four days earlier than did the checks. Salomone (1907) states that the stimulation of the vegetative portion of plants is greater than that of the grain. Comparison of the data in tables 7 and 8 shows that greater differences in the yields were obtained when the plants were harvested before they matured.

Manganese content of yellow leaves

Several investigators have reported that the yellow leaves of manganese plants contain more manganese than do the green leaves. The leaves of the plants grown on soil treated with manganese sulfate (page 385) were analyzed for their manganese content by the colorimetric method described in Bulletin 31 of the United States Bureau of Soils. The results are given in table 10:

TABLE 10. ANALYSES OF LEAVES OF WHEAT GROWN ON SOIL TREATED WITH MANGANESE SULFATE

Parts per million of manganese added	Manganese (in parts per million grams of dry matter) in		
	Green leaves	Yellow leaves	Medium yellow leaves
0	Trace	Trace	Trace
10	Trace	Trace	Trace
50	Trace	3.8	1.22
100	1.15	7.25	3.37
1000	1.95	11.25	3.12

If Aso (1902–03) is correct in stating that the colorimetric tests for the oxidizing enzymes showed that "the yellowish leaves of the manganese plants gave reactions of higher intensity than the green leaves of the control plants," it seems that the intensity of these enzymes is proportional to

the manganese content of the leaves. Woods (1899) states: "It has long been known that chlorophyll could be readily converted by oxidation, into a yellow coloring matter, xanthophyll." While a moderate stimulation of the oxidizing power of the plant juices may result beneficially, an excessive stimulation may result in the oxidation of the chlorophyll.

Relation of manganese to the oxidizing power of soils

In some cases the lack of fertility in a soil has been shown to be due to the presence of certain organic substances injurious to plant growth. Schreiner and Shorey (1909) found that when such soils are well aërated they become productive. Schreiner, Sullivan, and Reid (1910:44) state that the addition of manganese to soils promotes "the most active oxidation," and "by its strong oxidizing power . . . . . would render the injurious material in the soil harmless or even beneficial and by the oxidation of inert or rather stable organic matter might cause" a liberation of plant food. A brief study of the effect of manganese salts on the oxidizing power of soils has therefore been made by the writer.

Portions of Dunkirk silt loam were sprayed with solutions of manganese chloride, manganese sulfate, potassium permanganate and suspensions of manganese carbonate, and manganese dioxide, in quantities such that the manganese added was in the proportion of 10, 100, and 1000 parts of manganese per million of dry soil. It was thought that by spraying the soil a more uniform distribution of the manganese could be obtained. Consequently the calculated amounts of the salts were added to sufficient water to bring the soil to 25 per cent moisture content (dry basis). The spraying was done with a simple atomizer, made with two pieces of glass tubing of different bore and a wide-mouth bottle. It was found that the physical condition of the soil was very good when the water was added in this way. A determination showed that the moisture lost in the form of mist and evaporation during the treatment was negligible. The soils were stored in glass quart jars for about seven months.

To test the oxidation in the soil, 50 cubic centimeters of the following solution was added to 10 grams of the air-dried soil in a centrifuge tube:

10 grams aloin
200 cubic centimeters N/10 HCL
790 cubic centimeters distilled water

The tube was shaken for exactly one-half minute and was then placed in the centrifuge, which was started one minute after the solution was added. At the end of two minutes the electric current was turned off the centrifuge, and the speed was allowed to decrease gradually while a second test was started. Five minutes after the aloin was added in the first test, a portion of the supernatant liquid was poured into a colorimeter tube and the depth of color was compared with that of a standard.

This method will be found to differ considerably from that of Schreiner, Sullivan, and Reid (1910). The oxidation in the soils reported was so great that it was found necessary to use the method already described. The difference between the two methods is indicated by the following:

	Schreiner, Sullivan, and Reid	Deatrick
Time of test	2 to 3 hours	5 minutes
Concentration of aloin solution	0.125 per cent	1.0 per cent
Flocculating agent	C_2H_5OH	HCL

The standard used in the writer's experiments was a solution of aloin which had been completely oxidized with either manganese dioxide or nitric acid. The results were calculated on the basis of the oxidation in the untreated soil as 100.

The oxidation of phenolphthalin (made by reducing phenolphthalein with zinc dust and sodium hydroxide) was also used as a means of testing the oxidation in soils. The data are given in table 11. These figures indicate definitely that the addition of manganese salts to soils increases the power to oxidize organic matter such as aloin and phenolphthalin. It appears that the salts which are the most effective are the permanganate, the chloride, and the sulfate.

While the treatment with manganese dioxide seems to have interfered slightly with oxidation, it has been observed that soils treated with precipitated manganese oxides, instead of the pulverized pyrolusite, oxidize aloin readily. The oxidation in the air-dry soil from the field was very weak. The increase due to the moisture treatment alone is very noticeable. Since the soil contains no manganese, this is due to some other cause.

TABLE 11. OXIDATION IN DUNKIRK SILT LOAM TREATED WITH MANGANESE SALTS
(Tests made seven months after treatment)

Parts per million of manganese added	Relative oxidation	
	Aloin	Phenolphthalin
0	100	100
Potassium permanganate		
10	101	100
100	136	120
1000	444	200
Manganese dioxide		
10	93	100
100	94	100
1000	95	100
Manganese chloride		
10	105	100
100	113	125
1000	171	167
Manganese carbonate		
10	105	100
100	117	100
1000	128	142
Manganese sulfate		
10	105	100
100	136	130
1000	233	172

Adsorption of manganese

It had been noted that soil to which manganese salts were added developed a power to oxidize aloin in proportion to the length of time that the salt was in contact with the soil. In order to test this more accurately, portions of soil, the moisture content of which had been held at 25 per cent for seven months, were treated with solutions of manganese sulfate. The data, given in table 12, indicate that oxidation does not develop at once, but that it is greatest in the soil in which the manganese has been present for the longest time.

TABLE 12. EFFECT OF DURATION OF CONTACT OF SOIL WITH MANGANESE SULFATE, ON THE OXIDIZING POWER OF THE SOIL

Parts per million of manganese added	Date when manganese was added	Date when oxidation was determined	Relative oxidation
10	April 3, 1916	November 8, 1916	100
10	November 8, 1916	November 8, 1916	100
1000	April 3, 1916	November 8, 1916	185
1000	November 8, 1916	November 8, 1916	112

In order to test the adsorptive power for manganese, four percolation cylinders were filled with Dunkirk silt loam, a kilogram to each cylinder. The cylinders were labeled A, B, C, and D, respectively. To soils C and D calcium hydroxide was added at the rate of 10,000 parts of CaO per million of soil. Soils A and B were untreated. A solution of manganese sulfate containing 1000 parts per million of manganese was then percolated thru the soils after they had been saturated with distilled water. Each successive 100 cubic centimeters of the percolate was analyzed for manganese by the colorimetric method described in Bulletin 31 of the United States Bureau of Soils. The manganese content of the percolates, expressed in parts per million, is given in table 13:

TABLE 13. MANGANESE CONTENT OF MANGANESE SULFATE SOLUTION (1000 PARTS PER MILLION OF MANGANESE) PERCOLATED THRU DUNKIRK SILT LOAM

Successive 100-cc. portions of percolate	Manganese content in parts per million			
	A	B	C	D
1	0	0	0	0
2	Trace	111	0	0
4	62	286	0	0
6	500	400	Trace	0
8	625	417	62	Trace
10	715	455	154	92
12	715	500	218	167
14	715	525	256	143
16	715	555	357	222
18	770	475	357	91

The soils treated with calcium hydroxide precipitated more manganese than did the untreated soils. In the case of soil C, one liter of the solution was passed thru it before any appreciable amount of manganese appeared in the percolate. On air-drying these soils, C and D were found to have an intensive oxidizing power as compared with A and B.

Soils treated with 1000 parts per million of manganese in the form of pulverized pyrolusite were found not to have a strong oxidizing power. A solution of aloin, however, is rapidly oxidized when some of the pyrolusite is added to it. Colloidal manganese dioxide (from potassium permanganate and hydrochloric acid, purified by decantation) oxidizes aloin immediately. These phenomena, added to the fact that soils C and D developed the oxidizing power immediately in the presence of calcium, have led the writer to believe that the oxidation in soils due to manganese is due to the presence of manganese dioxide. In a solution of a manganese salt, manganic hydroxide is readily formed on the addition of an alkali. The formation of the oxide in soil to which a soluble manganese salt has been added, is directly proportional to the lime content, that is, the basicity of the soil. In the absence of an excess of an alkali form of calcium, the formation of the oxide of manganese is slower, for the stability of the soluble salts, as the sulfate and the chloride, is of course greatest in an acid solution. The salts of the weak acids, however, are not so stable, and when adsorption phenomena play a part, the salts are unstable even in neutral media. Thus, if pure, fine sand is treated with a solution of manganese citrate, this instability is soon demonstrated by the browning of the sand. This has been found to be the case with sand so treated and stored in a jar. On exposure to air, sand treated with the acetate and the citrate has developed a slight brown color.

Schreiner, Sullivan, and Reid (1910) apparently tested their soils immediately after adding the manganese salts. These soils were probably deficient in lime, and therefore the addition of manganese did not increase oxidation. The increase noted when hydroxy acids were added to these soils may have been due to the formation of the organic salt of manganese and the subsequent precipitation of the oxide from the less stable salt.

The formation of the dioxide, and the oxidation phenomena in soils as described, are analogous to the formation of calcium manganite (CaO.

MnO_2) and its use in the Weldon recovery process for the preparation of chlorine. The mixture of milk of lime and manganese chloride is termed *Weldon*, or *manganese, mud.*

Oxidation by plant roots

That roots of plants have an extracellular oxidizing power " may be demonstrated by the use of suitable chromogens," according to Schreiner and Reed (1909). In regard to their work on root oxidation in culture solutions containing alpha-naphthylamine, these investigators state (page 17 of reference cited) that " when the oxidation is performed by the growing roots of a plant, the oxynaphthylamine is deposited upon the surface of the roots in characteristic zones. . . . . . The zone of primary meristematic cells immediately back of the root cap is marked by a distinct narrow band of color." The browning of the roots of wheat in solutions of manganese salts resembles the staining caused by the oxidation of alpha-naphthylamine.

The reports of investigators indicate that such browning is characteristic of plants other than wheat, when grown in manganese solutions. This browning has been reported as consisting of a deposit of manganese dioxide. As far as can be ascertained by the writer, no proof has been offered for this statement. That the dioxide is formed, however, is indicated by the following: The black deposit is insoluble in water but dissolves in hydrochloric acid. When this solution is evaporated and the residue is fused with an alkali carbonate on platinum foil, the characteristic green color of the alkali manganate is developed. Furthermore, the blackened roots are capable of liberating chlorine from a solution of a chloride and sulfuric acid. If the plants thrive long enough in the manganese solution, the whole root system becomes blackened.

In writing of the deposit of manganese dioxide, Miss Houtermans (1912) states that the blackening is probably the result of enzymotic processes. The browning is the result of the oxidation which occurs on the surface of the root. The fixed alkali hydroxides precipitate from solutions of manganese salts manganous hydroxide, white, which readily turns to brown manganic hydroxide in the air or in contact with other oxidizing agents. Since manganous hydroxide is formed in the solution of a manganese salt by hydrolysis, it seems that it is deposited on the roots, as such, and

is there oxidized to a higher oxide, as the insoluble brown deposit. Soon after the heavy deposition of the oxide, disintegration of the root occurs.

Schreiner and Reed (1909) conclude that "the process of oxidation by roots is largely, if not entirely, due to the activity of a peroxidase produced by the roots." That the deposit is not caused merely by the instability of the manganese solutions in the presence of organic matter is indicated by the absence of any blackening on pieces of string or wood placed in them. A definite relation has been established between stimulants of this oxidizing power and stimulants of growth. Schreiner, Sullivan, and Reid (1910:9) state that "oxidation by plant roots is a factor which has considerable agricultural interest, especially from the viewpoint that such oxidation is able to change the organic matter in the medium in which the plant is growing and that processes promoting oxidation play a large part in the best methods of soil cultivation."

The effect of manganese on the oxidizing power of the roots of wheat seedlings was therefore investigated. Seedlings were set up as before in nutrient solutions (931 parts per million of salts) and grown for two weeks. Portions of these solutions were then treated with small quantities of the aloin solution and allowed to stand for twenty-four hours, and a comparison was then made of their relative oxidation. The results appear in table 14:

TABLE 14. Effect of Manganese Sulfate on Oxidation by Roots

Parts per million of manganese	Oxidation in solutions	
	With plants	Without plants
0	100	0
1	184	0
5	191	0
10	181	0
50	244	0
100	250	0
1000	206	167

In every case the cultures in which plants had grown oxidized the aloin more than did those in which no plants were grown. In fact, the aloin was but faintly oxidized in the checks, and with the exception of the one containing the greatest quantity of manganese the degree of oxidation

was considered as zero. When phenolphthalin was used as an indicator similar results were obtained, altho some trouble was experienced with these solutions because of the carbon dioxide content.

The bluing of gum guaiac was also used as an indication of the oxidizing power of the roots. The reagent, which was poured on the surface of the cultures, followed the path of the roots where it was oxidized. The objection has been raised that due consideration was not given to the oxidizing power of the manganese sulfate. It was found that a solution of gum guaiac is oxidized immediately by a solution of manganese sulfate containing approximately 10,000 parts per million of manganese. A solution of 1000 parts per million, however, gave only a slight bluing after three hours. Immediate bluing was obtained by the roots of plants grown in the presence of 10 parts per million of manganese in the form of the sulfate, while the bluing by the roots of the check plants was slow and not so intense.

Effect of manganese sulfate on soil bacteria

Numerous investigators have reported that the activity of the lower forms of plant life is increased by the presence of manganese salts. In order to test this point, cultures were set up to determine the effect of manganese sulfate on the ammonification of dried blood and the nitrification of ammonium sulfate in soil. These cultures were prepared from a fresh stock of Dunkirk silt loam, which had been passed thru a two-millimeter sieve and which contained 12 per cent (dry basis) of water. Portions of the soil each weighing 112 grams were placed in eight-ounce salt-mouth bottles. When properly treated the cultures were placed on the laboratory desk and covered with a moist pad, made of cheesecloth and cotton, to prevent the evaporation of water. It was found that in this way a large number of cultures could be kept at a constant moisture content with the expenditure of a minimum amount of labor. The cultures were run in quadruplicate and were incubated at room temperature. Two days after the cultures were set up, the soil in each bottle was stirred so as to insure uniformity in the distribution of the salts added. At the end of the incubation period, the soil in each bottle was stirred with 475 cubic centimeters of distilled water for three minutes and then allowed to settle for twenty minutes, and the supernatant liquid was filtered thru a Pasteur-Chamberlain filter. Aliquot portions of the filtrate were then analyzed for ammonia and nitrates. The ammonia was deter-

mined by adding concentrated sodium hydroxide, distilling, and titrating the distillate with tenth-normal hydrochloric acid. The nitrates were determined by the phenol-disulfonic-acid method, using the Schreiner colorimeter to read the intensity of color.

Ammonification.— To the soil used for ammonification tests was first added 0.5 per cent of dried blood. The manganese sulfate was added after the soil had been weighed out and placed in the culture bottles. Sufficient water was used as the solvent of the manganese sulfate to bring the soil in each culture to a moisture content of 25 per cent (dry basis). The cultures were incubated for one week, at the end of which extracts and determinations were made as described above. The results are given in tables 15 and 16:

TABLE 15. EFFECT OF MANGANESE SULFATE ON AMMONIFICATION OF DRIED BLOOD IN DUNKIRK SILT LOAM

(Cultures incubated for seven days)

Parts per million of manganese added	Nitrogen as ammonia, average of 4 cultures (milligrams)	Relative amounts
0	34	100
10	47	138
20	53	156
30	47	138
50	54	159
70	58	170
100	67	197

TABLE 16. EFFECT OF MANGANESE SULFATE AND 20,000 PARTS PER MILLION OF CALCIUM CARBONATE ON AMMONIFICATION OF DRIED BLOOD IN DUNKIRK SILT LOAM

(Cultures incubated for seven days)

Parts per million of manganese added	Nitrogen as ammonia, average of 4 cultures (milligrams)	Relative amounts
0	87	100
100	96	110
1000	109	125

The addition of manganese sulfate to the soil resulted in a positive stimulation in the ammonifying power. The addition of calcium carbonate resulted in a greater stimulation than that caused by the manganese alone. The stimulation of the manganese is not so great in alkaline soil as in soil deficient in calcium. This is as would be expected, for the solubility of the manganese is decreased.

Nitrification.— To the soil used for nitrification tests, 220 parts per million of nitrogen in the form of ammonium sulfate was added. The calculated quantities of solutions of manganese and ammonium sulfate were mixed, and were added to the soil in the culture bottles together with sufficient water to bring the soil to a moisture content of 25 per cent (dry basis). The cultures were incubated for four weeks. At the end of this time the extracts and determinations were made as described, and the results, expressed as parts of nitrates per million parts of dry soil, are given in tables 17 and 18. The experimental error of this determination is large, and the data given in the tables indicate that manganese sulfate in low concentrations did not affect the nitrifying power of the soil. In soils containing larger amounts of manganese, however, the nitrification was checked.

TABLE 17. EFFECT OF MANGANESE SULFATE ON NITRIFICATION OF AMMONIUM SULFATE IN DUNKIRK SILT LOAM

(Cultures incubated for thirty days)

Parts per million of manganese added	Nitrates, average of 4 cultures (parts per million of soil)	Relative amounts
0	234	100
10	236	101
20	252	108
30	197	84
50	156	67
70	136	58
100	122	52

TABLE 18. EFFECT OF MANGANESE SULFATE AND 20,000 PARTS PER MILLION OF CALCIUM CARBONATE ON NITRIFICATION OF AMMONIUM SULFATE IN DUNKIRK SILT LOAM

(Cultures incubated for thirty days)

Parts per million of manganese added	Nitrates, average of 4 cultures (parts per million of soil)	Relative amounts
0	344	100
100	326	95
1000	273	79

Conclusions

The experimental data here reported seem to justify the following conclusions:

1. Manganese salts added to water cultures affect the growth of wheat seedlings. The comparison of relative weights shows that when presented to the plant in high concentrations, both the sulfate and the chloride exert a toxic effect. In lower concentrations, manganese causes a marked stimulation.

2. The degree of toxicity is reduced by full nutrient solutions and the reduction is directly proportional to the concentration of the nutrient salts. Likewise, the food stored in the endosperms reduces the toxicity of the plant poiscn.

3. The toxic influence results in the browning of the roots and the bleaching of the leaves. The yellow leaves of the manganese plants contain more manganese than do the green ones.

4. Manganese salts added to soil form manganese dioxide in proportion to the basicity of the soil, and thus develop a power to oxidize organic matter as shown by the oxidation of aloin or phenolphthalin.

5. Manganese sulfate in water cultures stimulates the oxidizing power of the roots of wheat seedlings.

6. Low concentrations of manganese sulfate were found to stimulate the ammonification of dried blood in soil. The nitrification of ammonium sulfate was inhibited.

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THE PHYSIOLOGICAL ACTION OF NITROBENZENE VAPOR ON ANIMALS

WALLACE LARKIN CHANDLER

ITHACA, NEW YORK
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CONTENTS

THE PHYSIOLOGICAL ACTION OF NITROBENZENE VAPOR ON ANIMALS

THE PHYSIOLOGICAL ACTION OF NITROBENZENE VAPOR ON ANIMALS[1]

WALLACE LARKIN CHANDLER[2]

The present rapid development in America of industries which utilize large quantities of benzene or its derivatives in the manufacture of their products has greatly augmented the importance of the question of industrial poisoning. This is especially true of those industries in which nitrobenzene is used in some particular stage of a manufacturing process. Because of the pleasant odor and the retarded physiological action of nitrobenzene its toxic properties are not generally recognized, with the result that many workmen are constantly endangered by being either in actual contact with the liquid or exposed to its poisonous fumes. Furthermore, the physiological symptoms of nitrobenzene poisoning are not well understood, altho medical literature contains a large number of reports of such poisoning; and undoubtedly a large number of cases of industrial nitrobenzene-poisoning have been referred to other causes, the real cause having been obscured by the retarded and inconstant action of this chemical.

In the hope of obtaining more specific data regarding the physiological action of nitrobenzene, the initial experiments conducted by Dr. M. Dresbach and the writer on the investigation of nitrobenzene as a parasiticide (Chandler, 1917)[3] were continued. The present researches have resulted in findings which, it is hoped, may serve to make clear some of the factors regarding the action of nitrobenzene which hitherto have not been understood; for example, the cause of the "latent period," the reason for the inconstancy of certain symptoms, and the specific nervous centers involved. The work has also opened up new fields for investigation along the lines of neurology, physiology, and biochemistry.

The writer is indebted for advice and assistance to the following members of the faculty of Cornell University: Dr. M. Dresbach, of the Depart-

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[3] Dates in parenthesis refer to *Literature cited*, page 471.

ment of Physiology and Biochemistry; Dr. William A. Riley, of the Department of Entomology; Dr. E. M. Chamot, of the Department of Sanitary Chemistry and Toxicology; Dr. H. M. Kingery, of the Department of Histology; and Professor S. H. Gage, of the Department of Histology.

INTRODUCTION

Nitrobenzene (mononitrobenzene, nitrobenzol, oil of mirbane, artificial oil of bitter almonds, and so forth), $C_6H_5NO_2$, is a clear, straw-colored, oily liquid boiling at 210.9° C. and crystallizing in needles at 5.7° C.[4] It has the odor of oil of bitter almonds, and when undiluted has a pungent, unpleasant taste. It is soluble in all parts of alcohol, in ether, chloroform, benzene, oils, and liquid fats, and to some extent in lipoids. It is but slightly soluble in water. It has a vapor pressure of but 1 millimeter of mercury at 53° C. It is combustible, burning in the open air with a sooty, yellowish flame, and is explosive when heated to high temperatures such as would be obtained by throwing it on red-hot iron. It was first made by Mitscherlich (1834). At present it is manufactured on a large scale by "adding one part of benzene to three parts of a mixture of nitric acid (sp. gr. 1.40) and sulphuric acid (sp. gr. 1.84), this mixture being made up of 40 parts of the former to 60 parts of the latter" (Weaver, 1917). It is used in the manufacture of explosives (indurite); in the manufacture of anilin, which is used extensively in the making of dyes; in perfuming soaps, lotions, pomades, and other toilet articles; as a solvent in the manufacture of shoe polish, floor wax, and the like; in the manufacture of flavoring extracts and certain liqueurs; and for flavoring confections. It was recommended and used with friction as a parasiticide as early as 1863,[5] and has recently been recommended as a fumigant for the extermination of the external parasites of domesticated animals (Moore, 1916).

The poisoning effects of nitrobenzene were noted as early as 1856. Since that time, numerous cases of fatal poisoning in man have been reported, and several experiments on animals have been conducted for the purpose of studying the poisonous action of the chemical.

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[4] Determined experimentally. (See also Landolt, Börnstein, and Roth, 1912.)
[5] This recommendation stimulated investigations by Ollivier and Bergeron (1863) and by Guttmann (1866).

REVIEW OF LITERATURE

According to Letheby (1865), the ancient Greeks were apparently familiar with a substance the physiological action of which is similar to that of nitrobenzene. He states as follows:

It is said that Thrasyas, the father of botany, was so skilled in the preparation of drugs, that he knew how to compound a poison which would .... kill by a lingering illness. Theophrastus speaks of this poison, and says its force could be so modified as to occasion death in two, three, or six months, or even at the end of a year or two years; and the writings of Plutarch, Tacitus, Quintilian and Livy are full of instances of what seem to be the same kind of slow and occult poisoning.

However, nitrobenzene itself was unknown to modern chemistry until its discovery by Mitscherlich in 1834.

Most of the literature relating to the toxic properties of nitrobenzene consists of clinical reports of accidental cases of poisoning, and, from the standpoint of obtaining data on the physiological action of the drug, is unreliable for the reason that important information regarding the patient's "normal" condition is entirely lacking. Also, in the few experiments recorded dealing with its physiological action on animals, the drug was administered in the liquid form by either intravenous injections or introduction into the stomach by means of a tube, and very seldom by vapor inhalation. However, a review of some of these cases, both clinical and experimental, may serve to help interpret the results of the present experiments. Short abstracts of a few of these are therefore given.

CLINICAL CASES OF POISONING

Probably the most interesting clinical record is the case reported by Grafe and Homberger (1914) of a man who worked in a nitrobenzene factory filling containers with nitrobenzene. After working in this capacity for a period of fourteen days the man began to show symptoms of poisoning. These symptoms were a blue-gray color of the skin, headache, backache, stomach-ache, and vomiting. He continued to work for a few days after the onset of the symptoms. On Friday, October 27, 1905, he filled a double number of containers (ordinarily he handled 1600 liters), and on Saturday it was with difficulty that he continued to work. On Sunday he felt better, went into a saloon, drank two glasses of beer, and started to play cards, when he suddenly became ill. He went to see his father, but felt so ill indoors that he went outside for fresh air; immediately on coming into the air, however, he fell to the ground unconscious and was

carried back into the house. A doctor who was called gave the following report of the symptoms: skin blue-gray; pupils dilated; respiration retarded; pulse weak and irregular; patient unconscious. The man regained consciousness on the following day, and complained of pains in his head, his stomach, and his back. On July 30, 1906, the patient was found to have a chronic gastritis; his hemoglobin was 125 per cent and his red-cell count was 6,500,000. His intelligence and sense of perception had become dimmed. By July, 1908, his muscles had become atrophied, and he was extremely emaciated. His blood examination showed the following: red-cell count, 5,600,000; hemoglobin, 80 per cent; lymphocytes, 32 per cent; polymorphonuclear leucocytes, 47 per cent; eosinophiles, 20 per cent. By October, 1909, his memory had failed; otherwise he was in about the same condition as in 1908. In 1911 he was asked the date; he looked for a calendar and said that he did not know whether it was 1910 or 1911. His perception of distances had failed also. On October 4, 1912, he was visited by the doctor. When asked whether he recognized the doctor, he said that he had seen him before, but where and when he could not recall; thus he showed loss of perception of both time and space. He gave correctly the names of his children but could not remember which was the eldest. In March, 1913, his condition was about the same. If he wandered some distance from his home he was unable to find his way back. Several other incidents revealed the loss of perception of time and space.

Grafe and Homberger believe that the type of psychosis shown by this patient is identical with Korsakoff's syndrome, in which there is a loss of memory not only of things occurring before the accident but also of things occurring afterward. However, a careful analysis of the symptoms as recorded brings out the probability that the loss of perception of time and space was the principal feature; and this, according to Jelliffe (1913), indicates cerebellar lesions.

Taylor (quoted by Adams, 1912) reports the case of a young man who worked in a chemical laboratory. The report states that the young man placed one or two drops of nitrobenzene on his tongue in order to remove the odor of a pipe he had been smoking. He repeated this action one and one-half hours later. In a few hours he was seized with convulsions and became unconscious. The coma lasted for about six hours, but the patient died in about fifteen hours after regaining consciousness.

Another case of fatal poisoning resulting from a small amount of nitrobenzene is reported by Stone (1904). The report states that a strong man, weighing one hundred and sixty pounds, had stained the uppers of a pair of shoes with liquid shoe-blacking. He put the shoes on before they were dry and spent the evening in a café. About midnight he fell to the floor unconscious, and he died a few hours later.

These two cases are interesting from the fact that small quantities of the drug were able to produce death. Absorption in each case was probably facilitated by the presence in the blood of some solvent for nitrobenzene. In the latter case, the ingestion of alcoholic liquor undoubtedly facilitated the absorption thru the skin.

On the other hand, a number of cases have been reported in which the patient recovered after the ingestion of large quantities of nitrobenzene. Two interesting examples are as follows:

Dodd (1891) reports the case of a man forty-seven years of age, who ingested two drams of nitrobenzene. The resulting symptoms were vomiting, extreme cyanosis, fixed jaws, contracted pupils. The patient eventually recovered.

Schild (quoted by Adams, 1912) reports the cases of three girls who took nitrobenzene as an abortifacient. The approximate amounts taken were as follows: one ingested 5 mils, and recovered; the second ingested 16 mils, and recovered; the third took 16 mils, and died.

CLINICAL SYMPTOMS OF POISONING

Regarding the characteristic clinical symptoms of nitrobenzene poisoning, Türk (quoted by Roth, 1913) says:[6] "The clinical picture consists on the one hand of a greater or less stimulation of the gastro-intestinal tract; secondly, of changes in the blood which consist of the formation of methemoglobin and destruction of erythrocytes, with associated phenomena of high-grade cyanosis, blue skin color, later icterus, dyspnoea, etc." Weisstein (1892) says that there is great variation in the symptoms. He says that those symptoms which might be called characteristic are:

> Great dyspnoea, livid, cyanotic color of the skin, and characteristic bitter-almond-oil odor of the breath; even the urine may have this odor. In addition we may have symptoms which are not exactly characteristic, as they are inconstant, such as incoordination, hesitating speech, drowsiness, numbness, vomiting, convulsions, coma, dilation or contraction of pupils, or unequal dilation, nystagmus, irregular pulse. Death is due to a failure of respiration and circulation. In animals and in man the symptoms may appear early or late, even days late.[6]

[6] Translation from the original German.

Weisstein states further that the lethal dose depends on the form in which the dose is taken, the condition of the stomach at the time of taking, and other factors.

SEAT OF ACTION OF THE DRUG

Regarding the specific tissues acted upon by nitrobenzene, there has been much speculation. Roth (1913) writes as follows:[7] "The action of nitrobenzene depends, as is known, upon blood changes. Hence hematological changes have excited the greatest interest, tho in different cases the findings differ greatly." Some writers report pronounced hemolysis accompanied by leucocytosis, and those who have subjected the blood of patients poisoned by nitrobenzene to spectroscopic analysis have for the most part found an absorption band occupying nearly the same position as the methemoglobin band. Some have regarded this band as the methemoglobin band and have concluded that methemoglobin is formed in the blood in cases of nitrobenzene poisoning. Others claim that the band is distinct from the methemoglobin band and is peculiar to nitrobenzene alone. A discussion of these findings appears on a later page of this article. The following notes on the observations of blood changes in clinical cases may be of interest:

Roth (1913) reports the case of a woman who drank nitrobenzene to produce abortion. Her blood became dark chocolate in color. The red-cell count dropped from 4,662,000 to 3,840,000; the hemoglobin dropped from 98 to 80 per cent; the number of leucocytes dropped from 16,840 to 9400; and the lymphocytes rose from 14.4 to 22.3 per cent. There was no methemoglobin in the centrifugalized blood serum, but methemoglobin appeared in the red corpuscles. Hence Roth concludes that methemoglobin is formed inside the red corpuscles. He thinks that the formation of methemoglobin is due to the action of p-aminophenol, formed from the nitrobenzene.

Meyer (1905) reports the case of a patient who took about a teaspoonful of nitrobenzene, presumably to produce abortion, on June 15. On the 16th and 17th of the month the body temperature was 38° C. The red-cell count dropped to 2,180,000; the white-cell count dropped to 5200; the hemoglobin was 54 per cent. There was no morphological change in the red corpuscles.

[7] Translation from the original German.

Massini (1910–11) cites two cases. The first is that of a man thirty years old, a worker in a chemical laboratory, who on November 30 drank by mistake 30 mils of nitrobenzene. Vomiting was at once induced by giving $1\frac{1}{2}$ grams of copper sulfate in 50 mils of water. The color of the blood was dark brown until December 3. The red-cell count had dropped to 1,800,000 by December 9, but returned to normal by January 11. The white-cell count was 22,400 on December 7, and 6800 on January 11. The lymphocytes rose from 22.5 per cent on December 2 to 41.7 per cent on December 26. The polymorphonuclears dropped from 76.8 per cent on December 11 to 54.7 per cent on December 26.

The second case cited by Massini is one of chronic poisoning in a man thirty years old, who worked in a room with nitrobenzene. He was poorly nourished, the color of his skin was blue-gray, the spleen was enlarged, the urine was very dark, and urobilin was detected by spectroscopic analysis. The man was admitted to the hospital on June 4. The red-cell count was then 2,500,000, but it had risen to 4,300,000 by June 29. The white-cell count was 6000 on June 4, had risen to 8400 by June 8, and had dropped to 3800 by June 24. A microscopic examination of the blood revealed embryonal forms.

Bondi (1894) reports the case of a man twenty-five years old, who drank a "mandel liqueur" at nine o'clock in the evening. He was admitted to the hospital at four o'clock in the afternoon of the following day. The red-cell count was 6,340,000, the white-cell count 16,000; there was no methemoglobin; the hemoglobin was 112 per cent. Only one examination was made.

EXPERIMENTAL CASES OF POISONING

The literature dealing with experiments on animals is not very considerable. Only twice have intensive experiments been carried on, by Letheby (1865) and by Filehne (1878). It may therefore be well to include here a short abstract of the literature dealing with the subject from the experimental side.

The first experiment recorded was conducted by Jones (1857). He gave one dram of nitrobenzene to a rabbit, and reports that the rabbit was killed instantly. One-half dram of nitrobenzene in two drams of water, given internally, killed a cat within twelve hours. This writer gives no reference to earlier works, nor does he describe the symptoms

of nitrobenzene poisoning. He had been working on the toxic properties of a commercial oil of bitter almonds which was known to contain hydrocyanic acid. The experiments with nitrobenzene were conducted as a side issue and the purity of the nitrobenzene is doubtful.

Casper (1859) was led to experiment with nitrobenzene because in post-mortem examinations of cases of poisoning, the cause of which had been diagnosed as hydrocyanic acid, he often detected the odor of nitrobenzene in the tissues. He mentioned the desirability of learning whether this drug was poisonous, since it was being used more or less extensively in the perfuming of soaps, pomades, and the like, and stated that so far as he knew there was no account of it as a poison. His article contains a short account of the chemical and physical properties of the drug. In his experimental work he gave an ounce of nitrobenzene (purity not stated) to a rabbit in four separate doses at intervals of fifteen minutes. Within a few minutes after the final dose, the animal fell suddenly on its left side. Its pupils were dilated. Convulsions occurred which involved the entire body, and within a few minutes the animal was dead. The body was allowed to remain untouched for a period of twenty-four hours in order to simulate forensic post-mortem cases. It was then opened. No odor of nitrobenzene was detected either externally or in the lower part of the digestive tract, but when the skull was opened a strong odor of nitrobenzene was given off. This odor was so pronounced that a newcomer, who was wholly unaware of the experiment, at once spoke of "almond oil." The odor was detected in the blood, in the brain, and in other tissues. The body was placed in a cellar for two weeks and at the end of that time had lost but very little of the odor.

F. Hoppe (reported by Casper, 1859) introduced 20 mils of nitrobenzene into the stomach of a medium-sized dog. After a few hours the dog appeared stupid, and at the end of twelve hours it was found in a deep coma. Respiration was slow and the skin temperature was lowered. The animal was killed by pithing without causing convulsions. Blood drawn from the subclavian vein was dark brown in color, and the odor of nitrobenzene was detected in it. The same odor was detected in the urine, which was dark brown, in the bile, and in all the organs. The stomach contained a few drops of nitrobenzene, and the contents of the stomach were strongly alkaline. The blood retained the odor of the drug for several days. Casper concludes that these experi-

ments prove nitrobenzene to be a poison; and that a distinction between cases of poisoning by nitrobenzene and by hydrocyanic acid can be readily made, since the bitter-almond-oil odor due to hydrocyanic acid disappears within three or four days — the chemical (hydrocyanic acid) being destroyed by contact with the tissues — while the same odor due to nitrobenzene will persist for several days.

Ollivier and Bergeron (1863) were led to study the action of nitrobenzene from the same standpoint as was Casper — that is, because the drug was being extensively used in perfuming toilet soaps and in making flavoring extracts. It had also been recommended and used with friction for the cure of parasitic affections. These investigators argued that since nitrobenzene is readily converted into anilin thru the action of nascent hydrogen, it is conceivable that it may be changed into anilin in the human body, and anilin is a poison. They gave a guinea pig ten or twelve drops of nitrobenzene. The animal, after the initial agitation and profuse salivation, remained motionless for some time and then began to run about again without showing the least signs of ill effects from the drug. To another guinea pig they gave approximately three grams. The experiment was begun at 2.12 o'clock, and at 2.40 the animal exhibited tremors without excessive convulsions. The heart beats were very faint and the respiration was decidedly labored. At 3.10 the animal attempted to turn around and fell on its right side. The animal died a few minutes before 4 o'clock.

In another experiment Ollivier and Bergeron exposed the muscles of a frog's leg and placed on them a drop of nitrobenzene. The muscles remained sensitive to electric stimulations for a long time and did not show the slightest histological changes. The investigators then exposed the heart of a living frog and placed a few drops of nitrobenzene on it without obtaining the slightest modifications of the heart beat.

In a fifth experiment Ollivier and Bergeron gave a large, healthy dog six drams of nitrobenzene, and in a half hour an additional dose of five drams. The experiment was begun at 12.40 o'clock. The animal appeared agitated and secreted saliva profusely, but did not vomit. Finally it lay down in a dark corner and remained motionless for some time. At 1.20 it started to howl, appeared excited, and moved its head convulsively. Its tongue was hanging out and its eyes were wide and animated. This condition lasted for about six minutes, when the dog again became motion-

less. At 5 o'clock it showed tremors, and about an hour later its hind extremities were paralyzed. On the following morning it was found dead and rigid. A post-mortem examination showed the following: The blood was about normal, the cells being little altered, but the blood plasma contained fine, oily droplets which were recognized to be nitrobenzene. The meninges were congested, the veins turgid, the tongue and mucosae violet in color, and there was a stasis of the blood in the capillaries. The heart was dilated and filled with viscous blood, but there were no clots. The authors claim to have found anilin in some of the organs and in the blood, as well as nitrobenzene. They state that they had tested the nitrobenzene for the presence of anilin just prior to the experiments and had not found a single trace. Hence they conclude that their original assumption was correct — that nitrobenzene may be converted into anilin in the living body of an animal.

In another experiment these investigators caused a young dog to ingest a daily dose of from two to three grams of the drug for a period of sixteen days. They then killed the dog. They found no trace of anilin in any of the organs except the spleen and the liver.

From these experiments Ollivier and Bergeron draw the following conclusions: (1) that death due to nitrobenzene poisoning is delayed as compared with death due to an equal dose of anilin; (2) that nitrobenzene given in small daily doses is eliminated in part as such, and changed in part to anilin, which accumulates in the spleen and liver; (3) that the drug is in time eliminated as nitrobenzene and anilin, and is not changed into picric acid; (4) that animals poisoned by nitrobenzene die with symptoms of asphyxiation; (5) that the symptoms preceding death are similar to those in the case of anilin poisoning, except that the animal exhibits tremors, not convulsions of the whole body as in the case of anilin poisoning; (6) that nitrobenzene does not appear to cause any direct alteration of the blood, the muscles, the heart, the nerves, or other organs.[8]

In a further experiment with nitrobenzene, these authors placed guinea pigs, cats, and other small animals under a bell jar and introduced air saturated with the vapor of nitrobenzene, allowing a small opening for ventilation. Under these conditions they were able to produce death in from two to five hours, death being preceded by characteristic symptoms such as staggering, tremors, and paralysis of the hind legs.

[8] The staining of nerve cells by the Nissl method was not developed until 1885.

Letheby (1865) carried out a number of experiments for the purpose of studying the effects of nitrobenzene on dogs and cats. The drug was invariably administered by introducing it into the stomach. The results obtained in his various experiments were fairly similar; therefore the following report (page 49 of reference cited), which is quoted verbatim, may be taken as characteristic of the results obtained by him:

Experiment 2.— January 16th, 1862, at half-past three p. m., I gave half a drachm of nitro-benzole to a small terrier dog. The poison was poured into the animal's mouth; it caused discomfort, as if from the unpleasant taste, and produced a copious flow of frothy saliva. This, however, soon subsided, and for an hour there was no perceptible effect beyond a little heaviness of look. At the end of an hour the animal was sick, and after that it became sleepy. In another hour it was again sick, and again in a quarter of an hour. For four hours the animal lay on its side asleep, and then some water was given to it, which it took freely; from that time till midnight nothing appeared to be the matter with it, and the next morning it seemed to be quite well, and ate its food heartily. It remained thus all day, and was left at night apparently well, but the next morning at half-past six o'clock it was found upon its side insensible. The legs were in constant motion, as if the animal was running. The head was drawn back, and the muscles of the neck were rigid, as if in spasm; the eyes were open, the pupils were widely dilated, and the conjunctiva was insensible to the touch. The animal lay in this state for sixty-six hours, that is, nearly three days, and then it died as if from exhaustion. During the whole of this time the legs were in constant motion; there were occasional spasms, and then a sort of struggle for breath. The heart beat in an irregular, tumultuous manner, and the breathing was somewhat laborious. The total time which elapsed from the taking of the poison to the death was one hundred and four and a half hours.

The body was opened twelve hours after death. The brain and its membranes were very vascular; there was no odour of the poison in any part of the body; the lungs were slightly congested; the heart was full of blood on the right side, and there was a little on the left; the liver was of a deep purple colour; the gall-bladder was full of bile; the stomach was nearly empty, it only contained a little fluid and mucus; there was no sign of irritation. On analysis it yielded a trace of aniline, but no nitro-benzole; and nothing was found in the brain.

Letheby divided the action of nitrobenzene into two classes, characterized respectively by rapidly developing coma and by slow paralysis and coma after a considerable period of inaction. He summarizes the symptoms as follows (page 42 of reference):

When the effects were speedily fatal, the animals were soon seized with giddiness and an inability to walk. The weakness of the limbs first appeared in the hind extremities, and was manifested by a difficulty in standing; but very soon it extended to the fore legs, and then to the head and neck. There was complete loss of voluntary power; the animals lay upon the side with the head drawn a little back, and with the limbs in constant motion, as if in the act of trotting or running. The muscles of the back were occasionally fixed in spasm, and every now and then the animals had a sort of epileptic fit. They looked distressed, and howled as if in pain, and struggled violently; after which they always seemed exhausted, and lay powerless. The pupils were widely dilated, the action of the heart was tumultuous and irregular, and the breathing was somewhat difficult. For some time, however, the animals retained their consciousness, and gave signs of intelligence when spoken to; but suddenly, and often at the close of a fit, they became comatose, the eyes remaining open, although the conjunctiva was insensible to touch, and the movements of the limbs would nearly cease, the breathing became slow and somewhat stertorous, and the animals seemed to be in a

deep sleep. This condition generally lasted until they died — the duration of the effects being from twenty-five minutes to twelve hours after the administration of the poison.

When the action of the poison was slower there was often no visible effect for hours or days. At first there was always a little discomfort from the taste of the oil; but this soon subsided, and then the animals appeared to be in perfect health for a day or more; they would run about as lively as usual, and would eat their food heartily; but suddenly there would be a look of distress, and perhaps an attack of vomiting, and then a fit of epilepsy. When this had subsided the animals were weak, and sometimes they were paralyzed in the hind extremities. After two or three of such attacks, the loss of power extended to the fore limbs, and then they would lie upon the side in a perfectly helpless condition; after which the progress of the case was much the same as that already described, except that it was considerably slower: consciousness, for example, would be retained for days after the paralysis had set in; and although the animals were quite unable to stand, they would take food and drink when they were put into the mouth; in fact the condition in which they lay was most distressing; the look was anxious and full of fear, the limbs were in constant motion, and every now and then there would be a violent struggle, as if the creature was in a fit, or was making fruitless efforts to rise. This would last for days, and then there would be either a gradual restoration of voluntary power, with complete recovery, or death from exhaustion. The time which elapsed from the administration of the poison to the coming on of the first serious symptom — the epileptic fit — varied from nineteen hours to seventy-two: in most cases it was about two days, and the time of death was from four to nine days.

Letheby explains the long period of inaction as being due to the time required for the conversion of nitrobenzene into anilin. He does not explain the reason for the difference between the two types of effects. Guttmann (1866) thinks this is not the real explanation of the latent period, for if an animal were given only from thirty to sixty drops of introbenzene there would not be enough in the body to form anilin since nitrobenzene is continuously excreted by the lungs. Guttmann states, furthermore, that according to Bergmann two grams of anilin is not fatal to a small dog, and therefore from thirty to sixty drops of nitrobenzene could not be fatal if it were all converted into anilin.

Guttmann carried out experiments on frogs, rabbits, pigeons, and chickens. He states that in frogs he obtained paralysis of all movements and the abolition of all reflexes. This result was obtained whether the drug was given by mouth, by injection under the skin, or by exposure of the frog to the vapor under a bell jar. He concludes that since the muscles reacted to stimuli, the action of the drug was central, in contrast with that of curare and coniin, which act on the peripheral nerve structures. His paralyzed frogs did not recover. Dresbach (Dresbach and Chandler, 1917) obtained only depressant action on frogs, but in his experiments frogs that were paralyzed for from one and one-half to two hours recovered. Guttmann produced death in rabbits by placing in the mouth as little as $\frac{1}{2}$ mil of the drug. The symptoms reported were unsteadiness, staggering, loss of reflexes, wide pupils. Death resulted in each case in about

twelve hours. Post-mortem examinations showed dark blood, congestion of the brain membranes, and a pronounced odor of nitrobenzene in the tissues. All the organs were normal. (It will be remembered that Ollivier and Bergeron were unable to detect the odor of the drug in the tissues of a poisoned animal.) After introducing 1 mil of nitrobenzene into the mouth of a hen, Guttmann observed that the bird closed its eyes and had an unsteady gait, but recovered shortly. Later he gave 2 mils to the same bird, and it quickly became unconscious and died during the night. The brain was hyperemic, as in the case of the rabbits.

In regard to the action of the vapor, Guttmann states that Charvet breathed a " thick vapor " of nitrobenzene for several hours without ill effects, altho he had seen complete anesthesia and sleep produced in a dog after an exposure of one and a half hours to the vapor. He also says that Buisson denies that the vapor has any narcotic effect, and moreover that Ollivier and Bergeron killed cats and guinea pigs by exposing them to the vapor for from two to three hours. Guttman therefore placed pigeons under a bell jar and caused them to breathe the vapor of the drug. He observed no effects after an exposure of one hour, but produced death by an exposure of from two to three hours. He states that the symptoms are the same after vapor inhalation as after subcutaneous injections or after ingestion of the liquid. Guttmann did not observe convulsions in the animals poisoned, nor did he have a very long latent period as described by Letheby. He could not explain the latent period, but believed that Letheby's explanation was not correct, since in rabbits killed by ingesting four grams of nitrobenzene he could find no trace of anilin in the urine or in the organs. He used the calcium-hypochlorite test. He observes that Bergmann, who also could find no anilin in the tissues of the poisoned animals, ascribes the cause of the latent period to slow absorption of the drug; but Guttmann points out that this theory is not in accord with the cause of the rapid action which is often produced. He also found nitrobenzene in the blood of rabbits twenty-five minutes after subcutaneous injections.

Eulenberg (1876) killed a cat by exposing it to the vapor of nitrobenzene under a bell jar. He describes the symptoms as staggering, stupor, and so on. He states that the action of the vapor is more rapid than the action of the liquid. This contradicts Guttmann, who found the action of the vapor slower. Eulenberg could find no trace of anilin.

Filehne (1878) undertook experiments for the purpose of clearing up some of the questions concerning which the findings of other writers varied in their essential details. Those questions were: What is the reason for the latent period? Is nitrobenzene converted into hydrocyanic acid in the body? Is it converted into anilin in the body? What is the action of nitrobenzene on respiration and on the blood? Filehne also includes among his list of problems the following: spectroscopic analysis of the blood of animals poisoned experimentally by nitrobenzene; the action of nitrobenzene on blood outside of the animal; the action of nitrobenzene on the nervous system and on muscle tissue; and the therapeutic principles to be employed in treating cases of nitrobenzene poisoning.

Filehne maintains that the explanation of the latent period on the basis of time required for the absorption of the drug is not sufficient, since it cannot explain the extremely rapid course of the drug in some cases. Furthermore, Filehne found nitrobenzene in the blood within twenty-five minutes after it had been injected subcutaneously; he states also that animals heavily poisoned very quickly exhale nitrobenzene in sufficient amounts to perfume large volumes of water. He further claims that the latent period does not depend on an accumulative action of the drug, since a single drop introduced directly into the blood stream of a rabbit will kill the animal instantly. He thinks that the rapidity of the action depends on the rate in which the nitrobenzene passes from the blood to the central nervous system. In cases exhibiting rapid action the transfer takes place quickly and convulsions result (in dogs), while if the transfer takes place slowly the action is retarded and paralysis is the principal symptom. In the frog, Filehne observed only paralysis. He was able to produce rigor mortis also in the hind leg of a frog immediately after injecting nitrobenzene into the aorta, even in cases when the muscles had been severed from their connection with the central nervous system by cutting the ischiadic plexus, thus showing that nitrobenzene does exert a direct action on the muscle tissue. Filehne argues that the reason why Ollivier and Bergeron failed to show any action of the drug on the exposed frog leg was that the lymph in which the muscles are bathed may have served to exclude the drug from direct contact with the muscles. He writes that he himself has observed similar results when the muscles were thus protected.

Filehne claims that nitrobenzene is not converted into hydrocyanic acid in the body, since, in the first place, the blood of animals poisoned by hydrocyanic acid is red while that of animals poisoned by nitrobenzene is dark brown; then, too, the action of hydrocyanic acid on muscle tissue is different from that of nitrobenzene, as Filehne was able to prove by experiments on frogs; furthermore, Filehne was unable to detect the slightest trace of hydrocyanic acid in the blood or other tissues of animals poisoned by nitrobenzene, even by tests so delicate as to detect the drug in dilutions of 0.0002 per cent.

Nor will Filehne concede that nitrobenzene is converted into anilin in the body. He was unable to find any trace of it, as were also Bergmann and Guttmann. He shows that Letheby's method was at fault; that, according to Hoffmann and Muspratt, nitrobenzene when heated with alcoholic potash is converted into azobenzol, oxalic acid, and anilin. (Letheby apparently used the phenylisocyanide test, whereas Filehne applied the hypochlorite test.)

Regarding the action of nitrobenzene on the blood, Filehne found that in frogs and mammals the blood was dark brown after poisoning by nitrobenzene, except in the case of rabbits, which, he thinks, die before the drug can act on the blood. He could find no morphological changes in the blood-cells, but by spectroscopic analysis he found an absorption band occupying a position between C and D near the position occupied by the absorption band of acid hematin. He called this band the *nitrobenzol band.* It is possible that he was not familiar with the methemoglobin band, since the formation of methemoglobin was demonstrated only a few years prior to his experiments. Filehne was unable to produce the dark brown color in arterial blood by shaking it directly with nitrobenzene; he makes no statement regarding venous blood. By blood-gas analysis he demonstrated that the blood of animals poisoned by nitrobenzene had lost its ability to take up oxygen. He found the oxygen content of such blood to be less than 1 per cent, as against the normal 17 per cent, while the carbon dioxide content had increased in both absolute and relative amount.

Filehne states that the toxicologists have placed the convulsion-producing poisons in two categories: (1) those that produce convulsions in both frogs and warm-blooded animals (specific convulsion-producing poisons); and (2) those that do not produce convulsions in frogs but do produce convulsions

in warm-blooded animals, which convulsions are of a secondary nature (as in the case of asphyxia of the brain tissues) and not due to a direct action of the drug on the nervous system. He believes that nitrobenzene does not belong to either of these categories, since all the symptoms — nystagmus, pupil reactions, and the duration of the convulsions — point to a direct action of the drug on the central motor apparatus and yet the drug does not produce convulsions in frogs. He says (page 372 of reference cited),

> dass die bei Nitrobenzolvergiftung auftretenden Krämpfe nicht secundärer Natur sind, dass vielmehr das Nitrobenzol direct erregend auf motorische Centralapparate der Warmblüterwirke. Und zwar ist diese Erregung um so heftiger je schneller der Uebertritt des Nitrobenzols aus dem Blute in das Protoplasma der Ganglienzelle erfolgt.

He places nitrobenzene in the list with alcohol, ether, and the like, which exert a direct action on the central nervous system.

Regarding therapeutics in cases of nitrobenzene poisoning, Filehne says that solvents for this drug, such as alcohols, milk, and oils, are to be avoided. He recommends blood transfusions. He believes that the use of nitrobenzene for flavoring foods, in flavoring extracts, and in alcoholic drinks such as liqueurs, should be prohibited.

One other monograph may be mentioned, a paper by Zieger (1903). Zieger followed a method similar to the one used in the present research, but his technique was faulty in several respects and he used only a small number of animals — cats and rabbits. He says that nitrobenzol acts on the brain and respiratory organs and on the blood. He concludes that the vapor is not especially toxic when inhaled in amounts ordinarily met with, but that absorption of nitrobenzol from the skin can take place readily with serious results.

RÉSUMÉ OF THE LITERATURE

From the literature here reviewed it will be seen that the following points appear to be fairly well established:

1. That nitrobenzene exhibits toxic properties, whether it is ingested, applied to the skin, inhaled, or administered by subcutaneous injection.
2. That the size of the lethal dose is extremely variable.
3. That the symptoms of poisoning are inconstant.
4. That an interval of time (the latent period) often elapses between the administration of the poison and the onset of the symptoms.

5. That nitrobenzene is not necessarily converted in the body into anilin, hydrocyanic acid, or any other substance before it exerts a toxic action.

6. That nitrobenzene forms methemoglobin in the blood.

The following points, altho suggested, have not been satisfactorily explained:

1. The exact seat of action of nitrobenzene.
2. The cause of the latent period.
3. The reasons for the variability of the size of the lethal dose.
4. The reasons for the inconstancy of the symptoms of poisoning.
5. The significance of the various types of symptoms observed.

APPARATUS AND TECHNIQUE OF PRESENT EXPERIMENTS

APPARATUS

The apparatus used in these experiments was designed after a considerable period of experimentation with various devices; and, since it is such as may be used for investigating the physiological actions of a great many different gases, the principal parts are here described more or less in detail.

The apparatus consists primarily of a fumigation chamber, with accessory devices for saturating, dehydrating, and aerating this chamber. In addition apparatus was provided for determining the purity of the nitrobenzene used, such as devices for ascertaining the boiling point, the freezing point, and so on; and apparatus for determining approximately the amount of nitrobenzene vapor to a cubic foot of space within the fumigation chamber.

The fumigation chamber consists of a galvanized iron tank 60 inches long, 40 inches wide, and 30 inches deep. These dimensions were chosen so that the tank could be readily carried thru doorways. The chamber has a capacity of 43.75 cubic feet. A metal fossa, $\frac{1}{2}$ inch wide and $\frac{3}{4}$ inch deep, was constructed around the outer top edge, to receive the rim of the cover. When it was desirable to seal the tank, the cover was placed on and melted paraffin was poured into the fossa, thus rendering the tank air-tight. The cover is provided with two glass windows, one 8 x 10 inches and the other 12 x 18 inches. The larger window is removable, and fits into a slot in such a way that it can be sealed and unsealed readily;

paraffin is used for effecting an air-tight seal. It was thru this opening that animals were introduced into the tank, thus obviating the necessity of removing the entire cover each time. A small glass window was also built into one side of the tank, thru which observations of the temperature inside could be made. The tank rests on two runners, one of which is lower than the other in order to provide a slant to facilitate drainage of urine thru a small hole in one corner of the bottom of the tank. A false removable bottom 1 inch in height, made of strong wire of No. 2 mesh and well supported, was constructed in three pieces, for ease in handling. This false bottom serves to keep the animal from contact with its excretions. Two parallel steel supports are placed across the width of the tank $1\frac{1}{2}$ feet above the bottom, and on the middle of these supports rests a wire cage 8 x 8 x 10 inches. This cage serves to protect a small fan, which is connected to a motor on the outside by a shaft passing thru a tightly fitting collar in one side of the tank. This cage also protected a triangular strip of cheesecloth from which the nitrobenzene was evaporated. The container into which the cheesecloth dipped rested on an aluminum tray in the bottom of the cage. The inside of the tank and all its internal accessories were coated with paraffin in order to prevent rusting.

TECHNIQUE

Obtaining pure nitrobenzene

Practically pure nitrobenzene was obtained by redistilling the commercial liquid, at the temperature of the boiling point of nitrobenzene, until a product was obtained which proved experimentally to have a boiling point and a freezing point corresponding to pure nitrobenzene (page 412).

Aeration of the fumigation chamber

The tank was aerated by passing air saturated with nitrobenzene into it at a rate determined by the weight of the animal being fumigated. The air was saturated by passing it, after dehydration, thru a flask containing nitrobenzene and kept at a temperature of 50° C., and condensing it by passing it thru a series of U-tubes containing nitrobenzene. The final condensing tubes were placed inside the tank, so that the final condensing temperature equaled the temperature of the tank.

That this method for saturating air with nitrobenzene is practical was shown experimentally in the following way: A glass-stoppered U-tube containing a little nitrobenzene was dehydrated and weighed to constant weight. This U-tube was then placed in a constant temperature chamber, which was also a desiccator, with the final condensing tube, and air from this condensing tube was passed thru the U-tube for a given period of time. The U-tube was then reweighed, and the fact that it had neither lost nor gained in weight indicated that the air coming from the final condenser was saturated.

Maintaining constant temperature

A constant temperature ± 1 degree centigrade was maintained in the fumigation chamber by regulating the temperature of the room, it being found that a direct relation existed between these two temperatures.

Histological technique

In preparing sections for histological studies the following technique was employed.

The animal was quickly and painlessly killed by piercing the heart with a scalpel, since it was important that death should be produced without the use of drugs and in a manner which would produce a minimum shock. The body was opened immediately, a cannula was connected with the aorta, and a warm (normal body temperature) isotonic saline solution was transfused until all the blood was washed out. The saline solution was immediately followed by the warm fixing fluid, which consisted of 4-per-cent formaldehyde in a saturated aqueous solution of corrosive sublimate. The brain and the cord were then quickly dissected out, small pieces from each being placed directly in the fixing fluid and allowed to remain for twenty-four hours. The pieces were then washed in running water for twenty-four hours, after which they were carried thru 50-, 60-, 70-, and 82-per-cent alcohol. They were allowed to remain in 82-per-cent alcohol, to which was added a few drops of 5-per-cent alcoholic iodine, until the excess corrosive sublimate had been removed. The alcohol was changed twice a day for a time, and then as frequently as it became decolorized. The tissues were then dehydrated, cleared, embedded, and sectioned. The sections were cut 4 and 5 microns thick

and were fixed on slides by the usual methods. They were then cleared and carried down thru the various grades of alcohol to water, and then stained for ten minutes in hot (70° C.) 10-per-cent methylene blue in saturated anilin oil water (Rasmussen and Myers, 1916). When taken from the staining fluid they were hurriedly rinsed in a large volume of water, and were then placed directly in 95-per-cent alcohol where they were allowed to remain until they were sufficiently destained. They were then dehydrated, cleared in xylene, and mounted in balsam. Corresponding tissues from each of the poisoned animals and from the controls were carried thru the same fluids and stained on the same slides.

DESCRIPTIONS OF EXPERIMENTS

A large number of experiments were carried out. Since, however, the symptoms for each group of animals were in general fairly similar, so far as localizing the action is concerned, only two or three experiments from each group in which the animals showed typical symptoms are included in the descriptions. The other experiments included are those in which the symptoms were different in essential details.

DOG I (MALE DACHSHUND)

Weight of dog, 16.4 kilograms.

August 30, 1916 — Dog fumigated at 26° C. for a period of five and one-half hours.[9]
Time when fumigation was begun, 11.15 a. m.
Time when fumigation was finished, 4.45 p. m.

Observations: After having become accustomed to the strangeness of the fumigation chamber, the animal lay down and became quiet. At 2 p. m. it was observed that the dog had vomited, urinated, and defecated. At 3 p. m. the animal was seen to stagger when attempting to walk from one end of the tank to the other. At 4 p. m. the animal was found lying on its side; it was unable to lift its head; its respiration was labored. At 4.30 the condition was about the same. At 4.45 the animal was removed from the tank. The respiration was slow and regular, except for intermittent long, deep inhalations; the animal was unconscious;

[9] The chamber was thoroly dehydrated before the experiment was begun, but in this instance no time was allowed for saturation. Ordinarily sufficient time was given to insure saturation of the chamber before the animal was introduced.

the spinal reflexes were apparently gone; the conjunctival reflexes were present; there was profuse salivation. The muscles of the entire body were wholly relaxed when the animal was removed from the tank, but soon all of the legs became extended and rigid. This condition gradually passed off and the animal showed signs of recovery. By 11.30 p. m. the dog had regained consciousness and was able to stand on its feet. It walked slowly, with a trembling, staggering, uncertain gait and without aim.

August 31 — The animal was found to have greatly improved. It refused food, however, and howled when the back of its head was touched. It would press its head against the attendant's legs or other objects, and remain thus for hours.

September 1 — The dog was found normally active, eating meat and drinking water freely. No other effects followed.

September 22, 1916 — Dog fumigated a second time, this time at 23° C. for a period of six hours.
Time when fumigation was begun, 11.10 a. m.
Time when fumigation was finished, 5.10 p. m.

Observations: At 11.15 a. m. the dog was observed licking its chops. At 11.30 it was panting at intervals as if short of breath. At 12 m. it was slightly drowsy. At 12.05 p. m. it was unsteady, sitting on its haunches but keeping this position apparently with difficulty. At 12.10 it lay down in a natural position and closed its eyes; it would open its eyes when one rapped at the tank, but would immediately close them again. At 12.20 the dog's head was raised and the breathing was slow and labored. At 12.30 the animal appeared slightly confused, and uncertain as to the direction of the sound when one tapped on the tank. At 12.50 the animal stood up when called and walked across the chamber, but immediately went back and lay down again. From that time until 5.10, when it was removed from the tank, the animal lay quiet but alert as if sensing some danger. After the dog was removed from the fumigation chamber fresh vomit was found in the tank, which had probably been emitted while the chamber was being opened. A copious secretion of saliva was observed and the animal was slightly unsteady on its feet. It refused water.

September 26 — The animal had apparently recovered and no symptoms of the action of the drug appeared until on this day (four days after exposure to the vapor) when the attendant observed that the dog had difficulty in using its hind legs. An examination was made and the animal appeared normal. This was about 9 a. m. By 11 a. m., however, incoordination of the muscles of the hind legs was observed and the animal walked with a peculiar sprawling gait. This condition became more pronounced as the day advanced, and by 3 p. m. it was almost impossible to induce the animal to walk at all. Its tendency was to crawl into dark corners and hide. Finally the animal refused to remain on its feet, and when placed on its feet it would stumble and fall down again. However, at 4.30 p. m., after a considerable period of rest, the dog walked into its kennel with a slow, staggering, sprawling gait.

September 27 — There was evidence that the dog had thrashed about a good deal during the night and it was found lying prone on its side in the kennel. The animal appeared conscious, but was very irritable and thrashed about considerably. At 3 p. m. pronounced nystagmus was observed; the left pupil was dilated, the right pupil was contracted, and the jaws were set. At 4 p. m. the animal showed a tendency to remain on its left side; when turned on its right side, it executed a right-to-left rotation, finally coming to rest on the left side. The animal seemed to be conscious and wagged its tail when spoken to. The flexor muscles of the hind legs were in a state of tense tonic contraction, drawing the legs up against the body. The animal would neither eat nor drink. The anal temperature was 37.8° C.

September 28 — The general condition of the animal was about the same. The trunk muscles were tremulous, the extensor leg muscles contracted. The legs were withdrawn once or twice when touched, but finally they failed to react even to the prick of a pin, so tense was the muscular contraction. The animal made swallowing movements and could work its jaws to some extent, swallowing water when placed in its mouth. Nystagmus was not so pronounced. The anal temperature was 38.3° C.

September 29 — The animal appeared to be somewhat improved. Nystagmus was decreasing. The dog swallowed milk when placed in its mouth. The flexor muscles were relaxed. Clonic movements of the

hind legs were observed. The anal temperature was 39° C. The heart rate was increased only when the animal struggled, but was a trifle irregular.

September 30 — The animal was very much improved. It ate chopped meat and drank milk, and could raise itself a little. Its head waved about in an uncontrollable manner. The anal temperature was 38.5° C.

October 1 — Still more improvement was observed. The dog could almost regain its feet. It refused water, but drank milk without urging. In the afternoon the animal was able to stand on its feet; it walked eight or ten steps, and then staggered and fell. The anal temperature was 38.7° C.

October 2 — The animal walked fairly well, but staggered a great deal. It ate greedily.

October 3 — The animal had regained nearly the normal use of its legs and was found running about with other dogs. This dog finally recovered entirely and never developed any further symptoms.

It is interesting to note that this animal exhibited symptoms just the reverse of those described by Filehne as following a retarded action of the drug (page 424).

DOG II (MALE)

Weight of dog, 11.5 kilograms.

September 1, 1916 — Dog fumigated at 25° C. for a period of two hours and fifty-nine minutes.
Time when fumigation was begun, 12.40 p. m.
Time when fumigation was finished, 3.39 p. m.

Observations: Soon after being introduced into the chamber, the animal was observed to lick its chops; it panted at intervals; respiration was accelerated. At 1.45 the animal appeared restless, howling a good deal; it appeared to stagger. At 2.30 the animal was unable to remain on its feet; it lay on its side, with the extensors of all legs in tonic convulsions. At 2.50 the condition was about the same as at 2.30. At 3 p. m. the dog made sounds as if it was becoming anesthetized; there were clonic convulsions of the extensor muscles of the fore legs, and occasional clonic convulsions of the extensors of the hind legs followed by general abdominal

muscle tremors; respiration was quickened, with periodic long, deep inhalations; the dog was apparently unconscious, and could not be aroused; the eyes were open and winking; there was nothing abnormal about the pupils, and no nystagmus. At 3.04 the condition was about the same; the dog moaned at intervals. At 3.24 the respiration was 40, and increased in depth with periodic long, deep inhalations as before. At 3.25 there was opisthotonos, the convulsions lasting for about one-half minute and being followed by accelerated respiration. At 3.27 the respiration was 52. At 3.35 the respiration was shallow. At 3.39 the animal was removed from the tank; the muscles of the entire body were relaxed, but soon the leg muscles stiffened; the tongue and the lips were cyanotic. At 3.40 the respiration was irregular, gasping; the animal was given artificial respiration and oxygen, but it died at 3.50.

The body was opened immediately. The heart blood was of a chocolate color; the lungs were a dark gray; the intestines were hyperemic; the liver and the spleen were coffee-colored.

In this case the type of symptoms described by Filehne as following a rapid action of the drug were undoubtedly shown.

DOG IV (FEMALE)

Weight of dog, about 12 kilograms.

September 27, 1916 — Dog fumigated at 21.5° C. for a period of ten hours.
Time when fumigation was begun, 8.30 a. m.
Time when fumigation was finished, 6.30 p. m.

Observations: Immediately after being introduced into the fumigation chamber the animal lay down and went to sleep. It scarcely moved from this position during the entire ten hours; when the observer tapped on the tank the animal would open its eyes; when the tapping was loud it raised its head but seemed confused and could not follow the sound. At 4.30 p. m. the respiration was observed to be decidedly increased. At 5 p. m. the observer tapped loudly on the tank, and the animal opened its eyes but did not raise its head, tho it appeared normal. When removed from the tank at 6.30, the animal was lively, eating and drinking freely, and depositing a great quantity of apparently normal urine. This animal developed no symptoms of poisoning afterward.

DOG V (FEMALE)

Weight of dog, 11.2 kilograms.

October 26, 1916 — Dog fumigated at 20° C. for a period of twelve hours.
Time when fumigation was begun, 8.30 a. m.
Time when fumigation was finished, 8.30 p. m.

Observations: The animal rested quietly during the entire course of the experiment, and was removed from the tank apparently unharmed. It ate heartily of roast beef and showed no symptoms of poisoning during the next three days.

October 29 — The animal vomited when it was taken out of the kennel, but no other symptoms were especially noted during the day.

October 30 — The animal was found on its side and was unable to stand. The following symptoms were observed: lack of coordination of the muscles of the extremities; neck muscles rigid and head drawn back on the body; ventroflexion of back; fore legs drawn up to the body; one or both hind legs involved in clonic convulsions; nystagmus.

October 31 — The condition was slightly improved. The fore legs were drawn up as before; the hind legs were extended, but were flexed on the body. The right pupil was widely dilated and the left pupil was contracted; this is just the reverse of the pupillary reactions observed in Dog I. Nystagmus was still in evidence. The neck muscles were not so rigid. The dog was very restless all day, but quieted down toward evening. It swallowed milk when placed in its mouth.

November 1 — There were no signs of nystagmus. The general condition was very much improved. The dog swallowed milk when placed in its mouth. The leg muscles were not particularly involved. Both pupils were widely dilated. The animal appeared to be conscious but did not howl.

November 2 — The dog's condition was very much improved. It noticed the observer as soon as he entered the room. The animal took milk freely. Nystagmus was observed at times. The pupils were somewhat dilated. The animal was able to raise its head.

November 3 — The condition was still more improved. The animal drank milk and water readily. Its head was raised. Its fore legs were folded beneath the body, but were stiff.

November 4 — The animal was able to stand but was unsteady on its feet. It ate meat and drank milk and water.

November 5 — The condition was about normal. The dog's appetite was good. The heart and the respiration were apparently not affected in this case.

January 20, 1917 — Dog fumigated a second time, this time at 20° C. for a period of five hours.
Time when fumigation was begun, 2.45 p. m.
Time when fumigation was finished, 7.45 p. m.

Observations: As before, the animal remained quiet during the entire course of the experiment, and was taken from the tank apparently unharmed, and eating and drinking heartily.

January 21 — No symptoms had appeared by morning. At 8 p. m., however, the animal exhibited an apparent stiffness in the hind legs. This passed off during the night, and no further symptoms were developed until on the morning of January 24, when a loss of coordination of the muscles of the hind legs was observed and the animal walked with a sprawling gait very similar to that shown by Dog I. Toward evening this condition was much more pronounced, and it persisted during the course of two days altho the animal developed no further symptoms.

January 27 — All lameness was apparently gone, and recovery was complete.

DOG VI (FEMALE)

Weight of dog, 10.7 kilograms.

October 27, 1916 — Dog fumigated at 25° C. for a period of three hours.
Time when fumigation was begun, 3.05 p. m.
Time when fumigation was finished, 6.05 p. m.

Observations: The animal remained quiet during the experiment and was removed from the tank in a perfectly normal condition. It ate heartily of roast beef. It had developed no symptoms by November 3.

November 3, 1916 — Dog fumigated a second time, this time at 22° C. for a period of four hours and forty-five minutes.
Time when fumigation was begun, 3 p. m.
Time when fumigation was finished, 7.45 p. m.

Observations: The animal was removed from the tank apparently unharmed, and developed no symptoms during the night.

November 4 — At 8 a. m. the dog was running about in a lively condition and was apparently normal. At 2 p. m., however, the animal was found in convulsions; the legs, particularly the hind legs, exhibited tetany and the muscles of the abdomen quivered violently. By 6 p. m. the convulsions had become even more pronounced, and the animal refused food and drink.

November 5 — At 10 a. m. the animal was found with its body flexed to the left, and rigid; all the legs were rigidly extended; when an attempt was made to straighten the animal out, the head would crash violently against the floor and the animal would immediately return to its former position. At 2 p. m. the animal's condition had not changed and it was decided to attempt to relieve its condition by a blood transfusion. At 4 p. m. this operation was undertaken; the animal became anesthetized with ether very readily, and did not struggle on coming out of the anesthesia; approximately 200 mils of dark coffee-colored blood was drawn from the carotid artery of the poisoned animal, and 500 mils of defibrinated blood from a healthy dog was transferred thru the femoral vein. At 7 p. m. the animal was found in a stupor; the respiration was fairly regular. At 9 p. m. the respiration was very irregular and labored; at intervals of about one and one-half minutes there appeared incoordinated movements of the muscles of the diaphragm and the chest, each set working alternately with the result that no air was inhaled; these spasms lasted for from one-half to three-fourths of a minute, and at their height all the legs would move as if the animal were swimming, and would then become extended and rigid; the muscles of the abdomen would quiver, then the animal would give one or two deep gasps and regular respiration was resumed for a time but gradually became lessened in depth again until the incoordinated movements reappeared; an attempt was made to obtain a kymographic record of the respiration, but the animal became so active that this was impossible. At 10 p. m. the animal's condition was about the same, tho a slight improvement in the respiration was observed; the heart rate was 52, the respiration 30–40.

November 6 — The animal seemed not to be greatly improved; the respiration was irregular, with a tendency to return to the type observed the day before, but it never reached that type again sufficiently to give a good record. At 12 m. the anal temperature was 26.8° C.; the animal urinated and passed very dark soft feces; the external anal sphincter was relaxed, but the internal sphincter was about normal; the respiration was regular but very weak; the animal made swallowing movements and was given a very little water, which was swallowed with difficulty. At 12.30 p. m. the animal was placed in a warm room (30° C.); the respiration was fairly regular but weak, and the animal gave occasional gasps. At 2.30 p. m. the external temperature was rather low and the room temperature was therefore increased; the dog's respiration was 48, and was regular but very shallow; the heart rate was 64 and was very regular. At 3 p. m. 1 milligram of strychnin sulfate was injected; the anal temperature was 30.5° C., the external anal sphincter was still relaxed. At 4 p. m. the respiration had improved to some extent, but it became shallow again at 4.30; the rate was about 50 a minute; the heart rate was 75. At 5 p. m. the animal was found gasping weakly; the heart rate was above 100. The animal died at 5.10, apparently as the result of respiratory failure; the sound of the heart indicated that that organ was in excellent condition. At 6 p. m. the body was opened; the general condition of the organs was found to be good; the spleen and pancreas were of a dark blue color; the peritoneum was slightly hyperemic; the stomach and the intestines were slightly hyperemic, with occasional hemorrhagic areas possibly due to roundworms which were present in large numbers; the rectum contained a small amount of soft, brown feces. There was no nystagmus observed in this case, nor did the pupils appear to be involved.

DOG IX (MALE)

Weight of dog, ?. (The dog, which was a very small one, was not weighed. Its weight was probably about 3 kilograms, and it was completely free of excess fat. This dog had a severe Demodex infection.)

December 4, 1916 — Dog fumigated at 22° C. for a period of five hours.
Time when fumigation was begun, 12.30 p. m.
Time when fumigation was finished, 5.30 p. m.

Observations: The dog appeared restless during most of the time it was in the fumigation chamber. At 1.30 p. m. it had vomited. At 5 p. m. it was observed to be unsteady on its feet; it staggered and fell, regained its feet, and fell again. At 5.30, when it was removed from the tank, the animal was able to walk but staggered about very much as if it had been intoxicated with alcohol; it ate cooked meat.

December 5 — The animal was found lying on its side in a helpless condition; the tongue and the lips were cyanotic; the skin temperature was very low; the heart rate was 70, but was regular; the respiration was irregular, as if from disorganization of the respiratory center, and was difficult to count; the conjunctival reflex was good; the dog was unable to move its legs; tremors were observed in the leg muscles, the abdominal muscles, and the lips; the jaws moved incessantly, as if the animal was gasping for breath; the dog was placed in a warm room on a piece of cotton. The animal's condition remained unchanged during the remainder of the day; its respiration was always shallow and irregular. At 7 p. m. it was found dead. A post-mortem examination showed the following: heart distended and all the chambers filled with ante-mortem clots; these clots also appeared in the larger blood vessels; the stomach was very distended and was filled with gas and undigested food; the duodenum was filled with a sticky, bloody mucus; the jejunum contained a dark brown mucous substance; the blood was a trifle darker than normal.

In this case asthenia appeared to be the principal symptom. The action of the drug was rapid, but did not cause the type of convulsions described by Filehne as following a rapid action of the drug.

DOG X (FEMALE)

Weight of dog, ? (medium-sized).

December 7, 1916 — Dog fumigated at 20° C. for a period of seven hours and fifty minutes.
Time when fumigation was begun, 2.10 p. m.
Time when fumigation was finished, 10 p. m.

Observations: The animal remained quiet during the fumigation, and when removed from the tank at 10 p. m. it appeared entirely normal. No symptoms of poisoning appeared until two days later.

December 9 — At 9 a. m. the animal was apparently normal. At 3 p. m. it exhibited a weakening of the hind legs, and walked with a staggering, sprawling gait, showing a lack of coordination of the muscles of the hind legs; it had recently vomited. At 5 p. m. the animal was no longer able to walk, and the extensors of the fore legs were in tetany. At 6 p. m. the animal was no longer able to stand; nystagmus had appeared, and both pupils were dilated, the left more widely than the right; the dog drank a little milk.

December 10 — The general condition of the animal was about the same as on the preceding night. Nystagmus was slight. The dog drank milk and water in the morning, but refused both food and drink later in the day. The legs were extended; there was nothing definite about the extension of the legs, one or both of the hind legs sometimes being extended and rigid, and the fore legs sometimes being thus affected; at times the tetany would last for a long period, and again it would be of short duration. At times the head was drawn strongly backward, with the muscles of the neck rigid. The pupils reacted slightly to light. There was an odor of nitrobenzene on the animal's breath.

December 11 — At 8 a. m. the general condition of the animal was worse, but it was still conscious; all the legs were rigidly extended for minutes at a time, and the head was drawn backward; when this condition passed off the animal was left prostrated; the pupils were contracted unequally. At about 1 p. m. the animal passed about 100 mils of dark urine (the first passed since the fumigation). At 10 p. m. the pupils were about normal; the animal swallowed a very little milk and water when these were placed in its mouth; when disturbed, the animal would attempt to use its legs, and this resulted in a tetanic convulsion involving the muscles of the legs and the neck.

December 12 — During the night the animal passed about 100 mils of very dark urine (almost like black coffee). The animal had regained the ability to move its legs a little, tho an attempt to do so usually threw them into tetany of the type described above. At 11 a. m. the animal was found with all four of its legs in constant motion; these movements were fairly well coordinated and rapid, as in the act of running or swimming; they would increase in rapidity and violence until the animal was thrown into a convulsion which apparently involved every muscle of the

body; the legs were straight and the head was drawn down under the body between the hind legs; these spasms lasted for a few seconds, during which respiration ceased entirely; as the spasms passed off, the animal would give a short, hollow cry and resume the running movements, tho with evidence of exhaustion; both the heart rate and the respiration were rapid; if the animal was lifted up or its legs were held for a moment, the swimming or running movements would cease for a time; the excitement was very similar to postanesthetic excitement, except for the convulsive periods. At 3.30 p. m. the animal was found quiet and relaxed; the respiration was 35. At 5 p. m. the animal swallowed a little milk and water which were placed in its mouth. At 10 p. m. convulsions were observed which were of the opisthotonos type except that the muscles of the hind legs were relaxed; these convulsions appeared at intervals, and were induced if the animal was disturbed.

December 13 — The animal was able to swallow but a very little liquid food when this was placed in its mouth, and so had had little or no nourishment. It lay on its left side, with its head drawn back on its body, its fore legs extended and rigid, and one or both of its hind legs drawn up to its body. The respiration was slow, 16–20, and was deeper than normal; the heart was irregular, the rate being about 160; the tongue and the conjunctiva were slightly cyanotic. Toward evening the heart seemed weaker; the animal swallowed a little milk; it had passed very little urine, and the little that was passed was of a dark color. The cause of the color of this urine has not been determined; it was not hematoporphyrin, by the spectroscopic test.

December 14 — The animal was found dead. It died sometime after 11 p. m. of the preceding day. A post-mortem examination showed the following: lungs, hypostatic congestion of the left lobe; liver, congested and dark brown in color; esophagus and stomach, containing a little clear mucous substance; all other organs normal.

DOG XI (FEMALE)

Weight of dog, ? (small, about 8 kilograms).

January 5, 1917 — Dog fumigated at 20° C. for a period of three hours.
Time when fumigation was begun, 2.25 p. m.
Time when fumigation was finished, 5.25 p. m.

Observations: The animal remained fairly quiet during the fumigation and was removed from the tank at 5.25 p. m. in an apparently normal condition. It was lively, ate heartily, and showed no symptoms of poisoning. No symptoms developed during the next three days.

January 8 — When seen at 11 a. m. the animal was apparently well and normal. At 5 p. m., however, it exhibited a loss of coordination of the muscles of the hind legs, and had vomited at some time previously. At 8 p. m. it was unable to stand.

January 9 — The animal was found lying on its left side in a helpless condition; when placed on its right side, it struggled violently until it regained the left side; it refused cooked meat and water, but drank a little milk. At 12 m. nystagmus was observed; the pupils were normal; the animal ate a little cooked liver. By 3 p. m. nystagmus was very marked; the pupils were normal; knee-jerk reflex was good in both legs. When seen at 7 p. m. the animal tried to stand on its feet, but its hind legs were apparently paralyzed; when it did not succeed, it at once began to howl.

January 10 — The condition of the animal was about the same. It lay continually on its left side and was unable to move its body. There was a certain amount of rigidity of the leg muscles at times, but this was not well marked. Knee-jerk reflex was good. The animal ate cooked meat, and drank milk but no water. Nystagmus was not noticeable.

January 11 — The condition of the animal was slightly improved. It could move its legs a little. It ate meat and drank milk, but refused water (it was given meat and milk twice). The pupils were normal.

January 12 — The condition of the animal was much improved. It was able to lift its body on its fore legs and crawl about the cage, but the fore legs weakened quickly. The animal passed urine which was very dark. It ate meat greedily and drank some water.

January 13 — The condition was much improved. The animal was able to walk about very well, but its legs seemed weak and gave way at times.

January 14 — The condition was still further improved.

January 15 — The condition was apparently normal. The dog was turned loose with the other dogs.

In this case no definite convulsions were observed, the dominant symptom being paralysis such as was reported by Filehne as following a slow action of the drug.

DOG XVIII (FEMALE)

Weight of dog, ? (small, rather thin; heavy Demodex infection).

April 23, 1917 — Dog fumigated at 23° C. for a period of four hours.
Time when fumigation was begun, 2 p. m.
Time when fumigated was finished, 6 p. m.

Observations: The animal was restless for a time after being placed in the fumigation chamber, but soon became quiet. It was removed apparently unharmed, and never developed any symptoms of poisoning as the result of this fumigation.

May 16, 1917 — Dog fumigated a second time, this time at 20° C. for a period of five and one-half hours. (The dog was slightly fatter than when first fumigated.)

Time when fumigation was begun, 1.10 p. m.
Time when fumigation was finished, 6.40 p. m.

Observations: As before, the animal was a bit restless when first placed in the tank, but it soon became accustomed to its new environment and became quiet. It was removed from the tank apparently unharmed, showing no signs of nitrobenzene poisoning and drinking water freely.

May 17 — No symptoms had developed.

May 18 — The animal was found with its hind legs paralyzed, and there were evidences of its having thrashed about during the night. It drank milk and water freely and ate meat. It was placed in a padded cage.

May 19 — The general condition of the animal was worse. It could raise its head and wag its tail, but its legs were useless. It ate and drank. This condition remained about the same until May 22, when some improvement was noticed.

May 23 — The animal was found with its body raised on its fore legs, swaying from side to side, apparently making efforts to stand up but its hind legs were useless. The animal had not defecated since being placed in the cage, altho it was taken out several times for this purpose.

May 24 — The animal was very much improved. It could use its fore legs very well and had some use of its hind legs, but when it attempted to walk it staggered and fell, or rather tumbled to the floor, striking its jaws against the floor with considerable force. It appeared very nervous, and was always moving and fidgeting about, apparently unable to remain quiet at all. The animal defecated for the first time since the beginning of the experiment.

May 26 — The general condition of the animal was about the same. It was taken out on the lawn for exercise. In standing, its hind legs were spread far apart. It was unable to walk or to run, but it actually tumbled along, jumping high into the air and coming down on its head or its back, turning somersaults, or tumbling over sidewise. This dog was by nature playful and it had lost none of its playfulness as the result of the fumigation; its efforts to play always resulted in its throwing itself violently about. An interesting observation was the attempt of the dog to go toward any one when called; it made better progress in attempting to go in the opposite direction. It apparently was confused as to distances, and was wholly unable to make progress in a straight line.[10]

RABBITS I AND II, AND GUINEA PIGS I AND II

November 2, 1916 — Animals fumigated at 22° C. for a period of nine hours.
Time when fumigation was begun, 10.30 a. m.
Time when fumigation was finished, 7.30 p. m.

Observations: These animals were apparently normal when removed from the tank, and never developed any symptoms afterward.

[10] This animal was killed in February, 1918, and a histological examination of the cerebellum revealed a striking absence of Purkinje cells. Only from 5 to 10 per cent of the number found in a normal dog were present. The contour of the cerebellum was apparently normal, and those Purkinje cells which were present were scattered fairly uniformly thruout the cerebellum. The condition of the animal had never improved very markedly; and while it had learned many new tricks regarding locomotion, its actions were always typically those of a cerebellar animal.

November 18, 1916 — Animals fumigated a second time, this time at 24° C. for a period of nine hours and thirty minutes.
Time when fumigation was begun, 10 a. m.
Time when fumigation was finished, 7.30 p. m.

Observations: As before, these animals showed no effects of the drug, either during the fumigation or afterward.

RABBIT III AND GUINEA PIG III

Dec. 22, 1916 — These animals were placed together in the fumigation chamber at 5.15 p. m., and were allowed to remain there until 4 p. m. on December 23. The temperature of the chamber remained constant at 20° C. during the first seven hours, then it gradually dropped until at the end of the next seven hours it was 15° C., and then it rapidly rose to 20° C. again. During the second seven hours no air was introduced into the tank.

Observations: The animals nestled together and remained quiet during the entire experiment. A string was tied to the rabbit's leg, and every hour or so the animal's reflexes were tested. They remained good. Both animals were a trifle stupid when they were removed from the tank. They were offered food and water, but would not drink and barely nibbled at the food. Suddenly the guinea pig fell on its right side and was unable to regain its feet. When placed on its left side, it immediately turned again to the right side. Violent tremors were observed in all its muscles, and presently it was seized with convulsions; all the legs were rigid and the head was drawn back on the body. This spasm lasted but a few seconds, and when it ended the animal shook itself violently and then executed running movements similar to those described in dogs. These movements were extremely rapid and lasted until another convulsion appeared. At 8 p. m. the guinea pig seemed to be recovering and was able to raise itself on its fore legs. It remained quiet for some time, and when observed the next morning it was dead. A post-mortem examination showed the lungs to be distended and the air passages were filled with blood; the blood was dark brown; the liver was congested; the other organs were normal.

At the end of two hours the rabbit had developed no symptoms, and at about 6 p. m. it was again placed in the fumigation chamber. The animal reacted to the jerk of the string until about 9 p. m. It was then removed

from the tank and was found to be in a stupor; it was wholly relaxed and perfectly reactionless. It remained in this condition for a few hours, and then died, without any signs of convulsions.

GRAY RATS

(*Mus decumanus*)

Five young rats were placed together in a large wooden box having a capacity of 10 cubic feet. Fifteen drops of nitrobenzene were placed on a strip of cheesecloth and the cloth was suspended in the box, which was then closed for twelve hours. At the end of that time the rats were removed. The animals were all perfectly anesthetized, and three of them were reactionless. One died five hours later, and another was killed for the purpose of examining its blood; both of these had dark brown blood. All the other three exhibited either right or left rotatory (pinwheel) movements; one of them was seen to roll over and over for several feet before becoming exhausted. Two of these remaining three died without showing other symptoms, and one recovered (at least temporarily) and escaped.

Two adult rats of the same species were fumigated together in the regular fumigation chamber for three and one-half hours at a temperature of 23.5° C. When removed from the tank they were apparently unharmed. Both of these died two days later, probably from lack of nourishment since it was impossible to induce them to eat while in captivity.

WHITE RATS

It was found that white rats could not stand a fumigation at ordinary temperatures for longer than from one and one-half to two hours. However, the rats used in these experiments were infected with trypanosomes and spirochætes, and this fact may have had something to do with hastening the action of the drug. The rats that were still alive when removed from the tank showed only paralysis and usually died very quickly.

CAT X

September 26, 1916 — Cat fumigated at 17° C. for a period of five hours.
Time when fumigation was begun, 11.50 a. m.
Time when fumigation was finished, 4.50 p. m.

Observations: The animal lay down and remained quiet for about three hours, and then became restless for a time but soon became quiet again. When first removed from the tank the animal appeared well and started to walk away, but lost control of its hind legs and tumbled about for a moment, then became excited. It vomited (chunks of meat which had not started to digest), and then lay prostrate for about one-half hour. The lips and the tongue were cyanotic; the pupils were dilated and did not react to light. The animal's condition improved shortly and it again appeared well. On the following morning a quantity of sticky, bloody feces was found in the animal's cage; no further symptoms of poisoning had developed, however, nor did any symptoms appear during the next four days. At the end of this time the cat was found dead.

CAT XVIII

October 5, 1917 — Cat fumigated at 22.5° C. for a period of three hours.
Time when fumigation was begun, 9 a. m.
Time when fumigation was finished, 12 m.

Observations: The animal remained quiet during the fumigation and was removed from the tank apparently unharmed, but became slightly stupid toward evening. A sample of blood was taken and examined. It was dark brown and showed methemoglobin by spectroscopic analysis.

October 6 — The animal was found with well-advanced symptoms of nitrobenzene poisoning — nystagmus, paralysis of the muscles of the hind legs, and periods of excitation followed by prostration. The cat refused milk, nor was it possible to place any in its mouth. A sample of blood drawn from the ear was coffee-colored and showed the same spectrum as on the preceding day.

October 7 — The condition of the animal remained about the same. It lay on its side entirely helpless and apparently unconscious.

October 8 — The condition gradually grew worse and the animal died toward evening. A post-mortem examination showed a pronounced congestion of lungs and viscera, and the blood vessels of the neck were turgid with blood.

HEN V

March 21, 1917 — Hen fumigated at 30° C. for a period of six and one-half hours.
Time when fumigation was begun, 1 p. m.
Time when fumigation was finished, 7.30 p. m.

Observations: The bird was removed from the tank apparently normal except that it appeared a little stupid. The feces were formed when the bird was first placed in the fumigation chamber, but those deposited immediately after the bird was removed from the tank were soft, stringy, and slightly bloody.

March 22 — The bird appeared normal except that the neck feathers were constantly ruffled — a condition which induced such a belligerent attitude on the part of the other birds in the cage that this hen had to be placed by itself. No further symptoms developed until March 27, on which day the bird was found lying prone on its side and apparently unable to stand. When the bird was lifted it exhibited a circular rotation of head and neck; and when it was placed on its feet, the legs stiffened, throwing the bird backward.

March 28 — The bird's general condition was about the same. Nothing new was especially noted.

March 29 — The bird's condition had grown worse. The skin was cold, and the bird was placed in a warm room. There appeared frequent periods of excitation, during which the bird thrashed about a good deal.

March 30 — The bird was found lying on its left side, with its left leg extended and rigid and its right leg exhibiting violent tremors. The respiration was normal. The head was moving by jerks sidewise. When placed on its feet the bird lunged forward instead of backward. At 2 p. m. the bird swallowed some water when its head was placed in water and then released; it also swallowed a little moistened bread when this was placed in its mouth. Each attempt at swallowing was followed by excitation, during which the head was drawn back rigidly between the wings or revolved slowly, describing broad circles. When placed on its feet the bird lunged backward.

March 31 — The bird was again fed as described.

April 1 — The condition was about the same, altho the bird appeared stronger. When placed on its feet it attempted to walk, but the legs stiffened and the bird was thrown forward.

This bird never fully recovered. It was able to squat on its feet after a time, but refused to walk; when urged, it took two or three rapid steps and then tumbled over forward. It was unable to remain on a perch, falling either forward or backward. The wing movements were well coordinated. For a long time the bird was unable to eat without assistance, but it was finally taught to do so. The bird was killed on June 11, in order to make an examination of the brain tissues.

HEN VI

March 22, 1917 — Hen fumigated at 27–28° C. for a period of eleven hours.
Time when fumigation was begun, 10 a. m.
Time when fumigation was finished, 9 p. m.

Observations: The bird was removed from the tank apparently unharmed. The feces were as described for Hen V.

March 23 — The bird was apparently well, but not very active. It ate cracked corn and drank water. The neck feathers were ruffled.

March 24 — When first seen on this day (at 8 a. m.) the bird appeared normal. It was taken from the cage and placed on the floor. It was able to walk and run very well, but suddenly showed a tendency to give way to the left side; it flew to a perch 18 inches high, but was unable to retain its position; it fatigued very easily. At 10 a. m. the attendant reported that the bird had been in convulsions; it appeared normal except that it was a little dull. At 3 p. m. the bird appeared to be drowsy; it was removed from the cage and placed on its feet; it stood swaying from side to side; when it attempted to walk, it staggered and then swayed backward, taking several steps in an effort to catch itself; after this excitement its head was bent back between its wings. At 4 p. m. the bird was found lying on its side and was unable to stand; when it was picked up, its head rotated in a circle, sweeping the back and the wings. At 4.15 about an ounce of clear fluid came from the bird's mouth. At 5 p. m. periods of excitation were observed; the legs were in violent motion as in the act of running, and the head shook violently as if the bird were

trying to dislodge something in it; these periods of excitation were of short duration and were followed by periods of prostration lasting for several minutes, during which the muscles were wholly relaxed and the neck was limp; then with a sudden jerk, the period of excitation would appear again; this excitation could always be elicited by disturbing the bird; when the bird was placed on its feet, the legs stiffened and threw the body backward; the legs were bluish (they were pink normally); frequent movements of the gullet were observed, these movements often involving the mouth. At 5.15 another ounce of clear fluid came from the mouth. At 6 p. m. the bird made a violent effort to regain its feet; the wing movements were well coordinated but weak; this effort was followed by excitation during which the legs moved violently as described above.

March 25 — At 9 a. m. the bird's condition was worse; there was constant rotation of head and neck; convulsions occurred as before; when placed on its feet, the bird squatted quietly for a moment and discharged a large quantity of watery fluid from the anus, and then went into convulsions again. At 5 p. m. the bird was apparently better, and was resting quietly in an upright position. At 7 p. m. the bird was found in convulsions; the head was bent firmly on the venter (almost between the legs); the bird had no control of any muscle.

March 26 — In the morning the bird was found with all muscles relaxed except the neck muscles, which were rigid and held the head firmly against the venter. At 6 p. m. the bird was found dead. A post-mortem examination revealed a strong odor of nitrobenzene in all the organs; the crop and the gizzard were filled with cracked corn, which had not started to digest altho the bird had had nothing to eat during the preceding sixty hours: the other organs were about normal.

HEN VII

March 25, 1917 — Hen fumigated at 25° C. for a period of eight hours.
Time when fumigation was begun, 2.15 p. m.
Time when fumigation was finished, 10.15 p. m.

Observations: When removed from the tank the bird was a trifle stupid but was otherwise normal. It developed no symptoms of poisoning until March 30.

March 31 — The bird showed symptoms very similar to those described for Hen VI.

April 1 — The bird was found dead.

On March 27 (two days after the fumigation) this hen laid an egg. The egg was opened on March 29; a strong odor and a very characteristic taste of nitrobenzene were detected in the yolk, but the white did not contain more than a trace of the chemical. This phenomenon can easily be explained by the fact that nitrobenzene is soluble in fats, but is scarcely soluble at all in the white of eggs.

HEN VIII AND ROOSTER III

May 10, 1917 — Birds fumigated together, at 23° C., for a period of eight hours.
Time when fumigation was begun, 2 p. m.
Time when fumigation was finished, 10 p. m.

Observations: The rooster was found dead at the end of the fumigation period. The hen appeared slightly stupid when removed from the tank and became easily fatigued, but was otherwise normal. No further symptoms developed in the hen until on May 14, when it was seen to stagger on attempting to run. During the next few days the bird was very stupid. It did not eat much, staggered in attempting to walk, and fatigued easily.

May 25 — The condition of the bird was apparently normal again. No further symptoms ever developed in this bird.

PIGEONS IV AND V

June 11, 1917 — Birds fumigated at 24° C. for a period of six hours.
Time when fumigation was begun, 1.10 p. m.
Time when fumigation was finished, 7.10 p. m.

Observations: The birds were apparently normal when removed from the tank. They could fly and run easily.

June 12 — One of the birds showed the following symptoms: it was unable to fly, tho the wing movements were fairly well coordinated; in attempting to walk, it lunged forward and tumbled on its head; there was rotation of head and neck.

June 13 — The bird showing on June 12 the symptoms described, flew the length of the room along the floor, its head touching the floor. It probably had the use of its wings but could not direct the flying movements. The other bird showed symptoms of poisoning on this day. Both the birds were killed about noon, and the nervous tissues were fixed as described earlier (page 429).

OBSERVATIONS OF THE ACTION OF NITROBENZENE ON INSECTS

During the fumigation of the animals a number of external parasites dropped from the hosts. These were collected at the end of the fumigation period and observations were recorded regarding the action of the drug on them. Some of these observations were as follows:

FLEAS

Eighty-three fleas of the genus Ctenocephalus were recovered from the bottom of the tank after the fumigation of Cat X (fumigated for five hours at 17° C.). Most of these began to show signs of life in about one and one-half hours; they were put into a glass tube and placed in a warm room, and in about twelve hours all the fleas had recovered with the exception of about one-half dozen, which were stuck fast to the tube.

Nineteen fleas of the same genus were recovered in a stupefied condition from the bottom of the tank after the fumigation of Dog I (second fumigation, six hours at 23° C.). Three of these showed signs of life, and most of them recovered during the next twelve hours.

Seventy-six fleas of the same genus were recovered from the tank after the fumigation of three kittens for a period of four hours at 22° C. Some of these fleas showed signs of life when removed from the tank, and twenty of them recovered and lived for several days.

BITING LICE

A large number of biting lice (*Trichodectes subrostratus*) were recovered in a stupefied condition from the bottom of the tank after the fumigation of Cat X (fumigated for five hours at 17° C.). Nearly all of these recovered during the next twelve hours.

A large number of the biting lice of poultry (*Menopon gallinae, Menopon stramineum, Lipeurus heterographus*, and *Goniocotes gigas*) were recovered

from the tank after the fumigation of Hen V (fumigated for six and one-half hours at 30° C.). The lice were all apparently dead, showing no signs of life, at the end of twelve hours. At the end of eighteen hours, however, some of them were seen to be moving their legs. In Goniocotes these movements were rapid, and were very similar in character to the movements of the legs of poisoned guinea pigs.

Approximately three hundred biting lice, representing six species, were recovered from the tank after the fumigation of a chicken for a period of one and one-half hours at 20° C. Some of these insects showed signs of life when removed from the tank, and nearly all of them recovered entirely during the next few hours.

Nineteen specimens of biting lice were recovered from the bottom of the tank after the fumigation of Hen VI (fumigated for eleven hours at 27–28° C.). None of these showed signs of life when taken from the tank, and none recovered.

THE FOLLICULAR MITE

(*Demodex folliculorum*)

Two or three cases of mild infection of demodecic scabies in dogs apparently cleared up after fumigations for long periods at low temperatures. One of these cases was Dog V, which was fumigated twice — once for twelve hours at 20° C., and once for five hours at 20° C. These observations led to the following experiments for the purpose of determining the value of nitrobenzene in controlling demodecic scabies.

A special fumigation chamber was constructed in such a way that the animal's nose passed thru a rubber collar and remained on the outside of the chamber, and an attempt was made to fumigate the body of the animal without permitting it to inhale a large amount of the vapor. Morphine and chloral hydrate were given in order to cause the animal to remain quiet during the fumigation. A six-hour fumigation under these special conditions had no effect on the mites, nor was it possible to induce dogs to remain quiet without giving them large doses of the narcotics. The method was therefore abandoned.

Small pieces of skin heavily infected with *D. folliculorum* var. *canis* were placed in a petri dish in which there was a drop or so of nitrobenzene. The dish was then kept at a temperature of 30° C. for six hours. At the end of that time the mites were still alive.

It was observed that a 33-per-cent solution of nitrobenzene in olive oil would have no apparent effect on dogs if applied externally and if the animal was allowed to remain in the open air, in spite of the fact that an external application of a solution of this strength invariably killed cats and rabbits. Hence a small, short-haired dog [11] having a heavy infection of *Demodex folliculorum* was bathed thoroly and frequently with the 33-per-cent solution; but no improvement in the condition of the animal could be noticed.

OBSERVATIONS OF THE ACTION OF NITROBENZENE ON INTERNAL PARASITES

GAPEWORMS

(*Syngamus trachealis*)

Three chicks showing symptoms of gapes were fumigated together for two hours at 25–26° C. on June 23, 1917. Two of the chicks developed symptoms of nitrobenzene poisoning on June 24. One of these died on June 25 and the other on June 26. Two nearly mature pairs of *Syngamus trachealis* were recovered alive from the trachea of the former, and three living pairs were taken from the trachea of the latter. The third chick developed typical symptoms of nitrobenzene poisoning on June 26. By July 8, however, this chick had fully recovered from the effects of the drug, and it had also recovered from the gapes by July 8. The recovery from the gapeworms, however, cannot be attributed to the action of the drug on the worms, since with its improved environment it would in all probability have recovered anyway.

INTESTINAL WORMS

A number of roundworms (*Belascaris marginata*) were found in the feces of Dog III on the morning following a fumigation for five hours at 18° C. These worms were observed to be dead and their death was attributed to the action of the drug. However, roundworms of the same species were recovered, very much alive, from the intestines of nearly all the dogs examined, even in cases following long periods of fumigation.

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[11] The solution was not tried on long-haired dogs, nor was a stronger solution tried. The animal did not lick the solution off, presumably because of the burning taste of nitrobenzene.

COCCIDIA

Specimens of *Eimeria avium* in the oöcyst stage were recovered from the feces of Hen VII. These oöcysts appeared normal, and the development of sporocysts and sporozoites occurred as usual.

EXPERIMENT TO DETERMINE THE ACTION OF NITROBENZENE ON DIGESTIVE FUNCTIONS

Post-mortem examinations of animals poisoned by nitrobenzene usually revealed the fact that food which had been in the stomach for some days had not started to digest. A special experiment was therefore conducted in order to check these observations.

At 11 a. m. on October 3, 1916, four kittens, all from the same litter, were each given an equally large portion of boiled hamburg steak. At 11.10 three of these kittens were placed in the fumigation chamber, where they were fumigated for four hours at a temperature of 22° C.

At 2.20 p. m. (three hours and ten minutes after the fumigation was begun) one of the animals died. The other two were removed from the tank at 3.10 and showed well-advanced symptoms of poisoning. One of them died at about 4 p. m. and the other at about 5 p. m.

At about 5.30 p. m. the control kitten was killed with chloroform and a post-mortem examination was made of all four animals. The stomachs of the animals that had been fumigated contained the full amount of the hamburg steak eaten, and in no case had it even started to digest. The digestion of the hamburg steak in the stomach of the control animal was well advanced.

EXPERIMENTS TO DETERMINE THE ACTION OF NITROBENZENE ON BLOOD

BLOOD COUNTS

Two pups, from the same litter and about three months old, were kept under similar conditions,[12] and blood counts were made on each for several days in order to determine the normal counts. Each animal was then fumigated, on different days and for different periods of time, and the blood counts were continued. Always, of course, as soon as an animal developed pronounced symptoms of poisoning it refused food, and this interfered with exact comparisons. The results of these experiments are indicated in the following tables:

[12] These animals were fed twice a day, each receiving at a meal 40 grams of cooked liver, ¼ pint of milk, 50 grams of bread, and all the water it wanted.

DOG C (MALE — WEIGHT 2.7 KILOGRAMS)

Date of blood count (1917)	Red blood-cells (per cubic millimeter)	White blood-cells (per cubic millimeter)	Hemoglobin (per cent)
January 10	5,196,000	23,400	60
11	5,312,000	25,000	60
12	5,344,000	14,000	65
13	5,336,000	15,000	60
14	5,040,000	16,000	64
15	....	....	....
16	4,936,000	11,600	62
17	5,178,000	17,400	60
18*	5,472,000	16,600	63
19	5,496,000	16,860	62
20†	5,500,000	17,200	66
21	5,608,000	23,600	62
22	6,040,000	19,620	‡72
23	§7,144,000	24,400	80

* Dog fumigated for five hours at 20° C. on this date.
† Symptoms of poisoning appearing.
‡ The comparison standard was the methemoglobin standard, so that if methemoglobin is formed within the red blood-cells, as Roth claims, and these cells increase, it is not surprising that the percentage of hemoglobin also should increase.
§ Since the animal refused water and could be induced to take only a very little milk, it is probable that the rise in the red-blood-cell count was due to a concentration of the blood resulting from lack of water.

A microscopic examination of the blood of this dog showed that the erythrocytes were slightly distorted; they appeared loose and sac-like, and would not form rouleaux in fresh mounts.

DOG D (MALE — WEIGHT 2.5 KILOGRAMS)

Date of blood count (1917)	Red blood-cells (per cubic millimeter)	White blood-cells (per cubic millimeter)	Hemoglobin (per cent)
January 10	4,904,000	15,720	65
11	5,604,000	19,660	65
12*	5,296,000	14,660	66
13	4,600,000	12,660	65
14	5,446,000	14,060	66
15	5,000,000	11,200	64
16	5,040,000	11,860	62
17	4,798,000	12,740	62
18	4,712,000	11,660	60
19	5,024,000	11,600	58
20	4,974,000	11,200	85

* Dog fumigated for four hours at 20° C. on this date.

This animal showed a slight drop in the red-cell count on the day following the fumigation, but this was not sufficiently great to be of any importance. The animal developed no very pronounced symptoms of poisoning. Dog C, on the other hand, did develop pronounced symptoms, and died on the evening of January 23; but Dog C had been fumigated for four hours at 18° C. on December 12, 1916, as well as for five hours in this experiment. As the result of the first fumigation, however, the animal was apparently unharmed, nor was there any change in the blood counts following the first fumigation.

SPECTROSCOPIC EXAMINATION OF THE BLOOD OF ANIMALS POISONED BY NITROBENZENE

A cat was fumigated for a period of three hours at a temperature of 23.5° C. Shortly after the fumigation a sample of blood was taken, diluted with distilled water, and examined spectroscopically. When the concentration was just sufficient to cause the oxyhemoglobin bands to disappear, a distinct band appeared between C and D, apparently in the exact position of the absorption band of methemoglobin. When the sample of blood was sufficiently dilute to cause the oxyhemoglobin bands to stand out clearly, the absorption band between C and D disappeared or was very faint. The undiluted blood was coffee-colored, and the diluted blood had the appearance of methemoglobin blood.

A young dog, a cat, a rabbit, a guinea pig, a chicken, and a pigeon were placed together in the fumigation chamber and fumigated for a period of three hours at 22.5° C. At the end of the fumigation, a sample of blood was taken from each and examined spectroscopically. The cat's blood showed the above-described band faintly; the guinea pig's blood showed the band very distinctly; the samples from the other animals failed to show the band. On the following day, blood samples were again taken and examined. The sample from the cat showed the band more markedly than on the preceding day; the sample from the guinea pig did not show the band at all, nor did the samples from any of the other animals.

A sample of blood was taken from a healthy cat and diluted with about fifty volumes of distilled water. The diluted blood was then shaken in

a test tube with a few drops of nitrobenzene. When examined spectroscopically, the sample showed no trace of the band, but only oxyhemoglobin. The sample was allowed to stand overnight, but the band even then failed to appear. Another sample was taken, diluted as before, and shaken with nitrobenzene. It was then placed in an incubator at a temperature of from 37° to 38° C. The methemoglobin band, above described, made its appearance at the end of four hours. However, since no control sample was incubated at the same time, this test is not a positive proof that nitrobenzene can form methemoglobin in blood outside of the animal.

The results described above agree fairly well with the findings of Filehne and others. There has been some disagreement regarding the nature of the band in question; however, a sample of methemoglobin prepared in the laboratory showed an absorption band in exactly the same position as that occupied by the "nitrobenzol band."

HISTOLOGICAL EXAMINATION OF THE TISSUES OF ANIMALS POISONED BY NITROBENZENE

DOGS

Four half-grown dogs, all from the same litter, were kept as nearly as possible under the same conditions. On January 24, 1917, three of them (Dogs E, F, and G) were placed together in the fumigation chamber and fumigated for a period of five and one-half hours at a temperature of 20° C. They were removed from the tank at 10 p. m., apparently unharmed.

On January 25 Dog F showed a slight lameness, hid himself away in a dark box, and did not eat well. The other two animals were apparently normal.

On January 26 all three of the dogs were found to have developed pronounced symptoms of nitrobenzene poisoning. The symptoms were of the same general character in each, but were more advanced in Dog F. All the animals were able to crawl about; they had a partial use of the fore legs but were not able to use the muscles of the hind legs. The knee-jerk reflex was good in each of the animals. There appeared an incoordination of the muscles of the neck, but there were no signs of

nystagmus, of abnormal pupil reactions, nor that the animals had vomited. All the animals drank milk, and Dogs E and G ate some meat.

On January 27, at 8 a. m., Dog F was found completely paralyzed except for slight movements of the hind legs, and there was a copious secretion of saliva. The knee-jerk reflex was good in both legs. At 9.30 a. m., this animal was howling excitedly. When disturbed it went into respiratory convulsions similar to those described for Dog VI (page 437). The animal was killed at noon and its tissues were fixed according to the methods described earlier (page 429).

Dog E refused food and water on this date, was wholly helpless, and howled incessantly. At 3 p. m., three hours after Dog F was killed, this animal was killed and its tissues were fixed in the manner described.

Dog G took milk in the morning on this date, but refused it at night. It exhibited the running movements of the legs described for Dog X (page 440), and howled a good deal.

On January 28 intense excitement was shown by Dog G. Its legs were moving rapidly with the running movements already mentioned. These movements continued for long periods at a time, and then the leg and the abdominal muscles would stiffen in violent convulsions; the head thrashed about and the animal gave guttural sounds as if worrying a rat; finally the animal would grasp part of its bedding with its teeth and hold it firmly for a moment, during which time respiration would cease, and then, after a few gasps, the running movements would begin again. At times the animal shook its head vigorously, as if trying to get rid of something in its ear. This dog and the control, Dog H, were killed in the course of the morning and their tissues were fixed, as nearly as possible, after the same manner as were the tissues of Dogs E and F.

Corresponding pieces of tissue from the different levels of the central nervous system of each of the four animals were carried thru the same fluids, and were finally stained and mounted on the same slide, as described on page 430.

No histological changes could be observed in the cells of any part of the central nervous system, except in the Purkinje cells of the cerebellum. The changes in these cells were typically chromatolytic degenerations.

PLATE VI

1–4, Photomicrographs of Purkinje cells from the cerebella of four dogs of the same litter. x 525

1, Normal cells from control animal. The presence of tigroid bodies (Nissl bodies [N]) is to be noted

2, Cell from animal poisoned by the vapor of nitrobenzene, showing the first stages of chromatolytic degeneration. The much swollen cell-body, and the absence of tigroid bodies except a few in the vicinity of the nucleus, are apparent

3, Cells from animal poisoned by the vapor of nitrobenzene, showing (a) the swollen cell-body and the absence of tigroid bodies, and (b) a homogeneous appearance of the cytoplasm and the absence of tigroid bodies

4, Remains of a Purkinje cell which has undergone chromatolytic degeneration. (From the cerebellum of a dog poisoned by the vapor of nitrobenzene)

5–6, Photomicrographs of motor cells from the ventral horn of the cervical cords of two dogs from the same litter. x 525

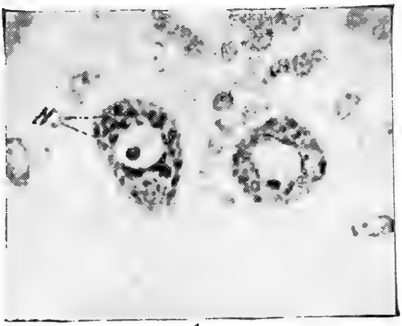
5, Normal cell from control animal

6, Cell, apparently normal, from animal (Dog F) poisoned by the vapor of nitrobenzene

7–8, Photomicrographs of sections thru similar convolutions of the cerebella of two dogs. x 60

7, From control animal, showing the presence of Purkinje cells (P) and a normal cortical area (c)

8, From animal killed nine months after being poisoned by the vapor of nitrobenzene (Dog XVIII), showing the absence of Purkinje cells and a much atrophied cortical area



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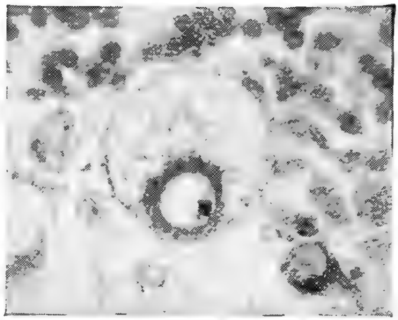
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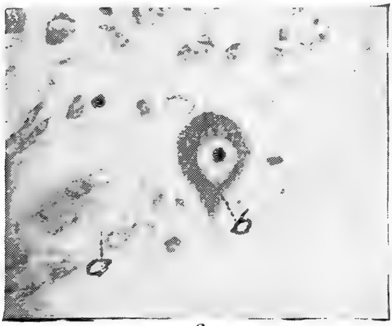

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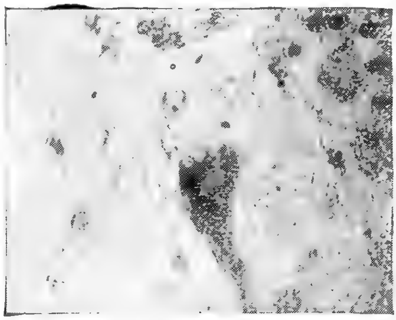
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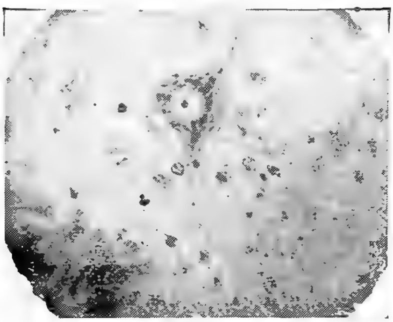
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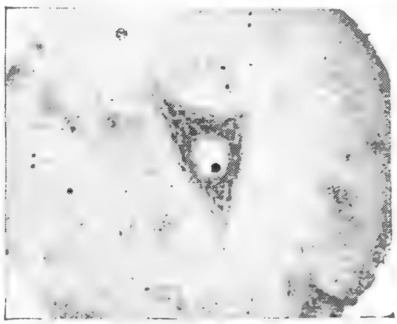
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The Purkinje cells from Dog F (Plate VI, 2) were greatly swollen, and the Nissl bodies (tigroid bodies) were almost entirely absent. There was no stainable substance near the periphery, and that around the nucleus was massed and indefinite. Some of the Purkinje cells from Dog E were like those from Dog F; others were very much shrunken, about one-half "normal" size, and the whole was a darkly stained, indefinite mass with the nucleus almost obliterated. The Purkinje cells from Dog G were all very much shrunken (Plate VI, 4), and no Nissl bodies were to be seen. There was a small amount of stainable substance, massed and clinging about a much-shrunken nucleus. In many cases the nucleus had disappeared, and in numerous instances the entire cell seems to have disappeared. The Purkinje cells from the control animal, Dog H, were all apparently normal, the tigroid bodies staining excellently (Plate VI, 1).

The above experiment was repeated, and this time two controls were used instead of one. One of the poisoned animals was killed shortly after the first appearance of the symptoms, and only a few of the Purkinje cells from this animal showed degeneration. Another one of the animals was killed before the symptoms were very far advanced, and in this case but few of the Purkinje cells looked wholly normal and some of them showed definite chromatolytic degeneration. The third poisoned animal was killed after the symptoms were well advanced, and the cells from this animal had become so thoroly degenerated that there was scarcely anything left of them but irregular blotches. The Purkinje cells from the control animals were all apparently normal.

Sections were made, stained, and mounted on the same slide, of the following additional tissues from the control animals and from the animal in this later experiment in which the symptoms of poisoning were well advanced: liver, spleen, thyroid, adrenal gland, duodenum, and rectus femoris muscle. No signs of degeneration could be observed in any of these tissues, but there appeared to be a slight hyperemia of the liver, the duodenum, and the rectus femoris muscle; these tissues were dissected out before the infiltration of the saline solution, so that the blood remained in them.

BIRDS

Two pigeons were fumigated with nitrobenzene, and when the symptoms became pronounced, they, together with a control, were killed by clipping

off their heads. The cerebellum was hurriedly dissected out and small sections from different parts were placed directly into the fixing fluid. The remainder of the technique was the same as that employed in the case of the dogs. The same degenerative changes in the Purkinje cells were found as were found in the case of the dogs. The Purkinje cells from the control bird were normal.

Two chickens, poisoned and killed in the same manner, showed the same type of degeneration in the Purkinje cells as is described above, while the cells from the control bird, stained and mounted on the same slide with those from the poisoned bird, were apparently normal.

THE SYMPTOM COMPLEX OF NITROBENZENE POISONING

Unlike Letheby and Filehne, the writer has been unable to divide the symptom complex of nitrobenzene poisoning into two types — that accompanying a rapid action of the drug, and that accompanying a retarded action. As a matter of fact, the symptoms are never sufficiently uniform in any case, whether the action is slow or rapid, to permit of classification into types. There is a probability, however, that the symptom complex may be somewhat different in widely separated groups of animals; but this can be determined only by a summation of all the symptoms observed in experiments on a large number of individuals from each group.

So far as has been observed by the writer, the dominant symptom in frogs and in insects is a general depression, tho in insects a tremulous movement of the legs has also been observed. In birds and mammals, one or more or all of the following symptoms may appear in acute cases of poisoning by the vapor of nitrobenzene: cyanosis, nausea, vomiting, ataxia, asynergia (distinguished from other types of cerebellar ataxia in that there appears a retro- or propulsion in an antero-posterior plane instead of a lateral, the legs appearing as if either running away from the body and throwing the animal backward, or failing to keep up with the body and throwing the animal on its head), impairment of digestive functions, nystagmus, equal or unequal dilation or contraction of the pupils, irritability, tenderness of the occiput (headache), unconsciousness, hallucinations, adiadochokinesis, slowing of the pulse rate, irregular and weakened respiration, palpitation of the muscles, rapid (running) movements of the legs, rotation of the head and neck describing broad circles, rotation of the body around its longitudinal axis, asthenia, and the nitro-

benzene breath. In chronic cases the symptoms which persist are: asthenia, ataxia, and (described in man) anemia, malnutrition, and Korsakoff's psychosis.

INTERPRETATION OF THE SYMPTOMS NAMED

While there is scarcely a single one of the symptoms described above that may not be referred to disorders of the central nervous system, still there is no doubt that nitrobenzene exerts a more or less serious local action on other tissues. The cyanosis observed in most cases of acute poisoning is undoubtedly due to a direct action of nitrobenzene on the blood; the blood has a dark brown color, and the presence of methemoglobin is demonstrable, at least in some cases, by spectroscopic analysis. Just how the changes in the blood are brought about is not definitely understood. Roth (1913) thinks that the nitrobenzene is converted into paraminophenol and that the latter drug acts on the red blood-cells, forming intracellular methemoglobin; he found no methemoglobin in the serum of certrifugalized blood. Türk (cited by Adams, 1912) says that not only is there a forming of methemoglobin, but there is also a destruction of the erythrocytes, due, he thinks, either to intravascular hemolysis or to a hyperfunctioning of the blood-destroying organs. That methemoglobin is formed, in certain cases, was demonstrated by the writer's experiments; the writer was unable, however, to demonstrate the destruction of erythrocytes, altho some morphological alterations of these cells were apparent. Also, Filehne (1878) has shown that nitrobenzene has a direct action on the muscle substance, causing the muscle to contract in rigor mortis; even the heart muscle was affected, according to him. Certain it is that nitrobenzene has an irritating action on the tongue and the mucosae; and, since it passes unchanged readily from the blood to other tissues, it is not impossible that it may have an irritating action on the deeper tissues also. However, if the symptoms produced are due to a direct action of the drug upon the blood, why, then, should there be such a long latent period in most cases? Furthermore, if the symptoms are due to a direct action of the drug upon muscles, glands, or abdominal organs, then these tissues should show histological changes; but the writer has failed to find anything more severe than a slight hyperemia, the cause of which may be easily explained on the basis of the hyperactivity of the organs concerned.

Disturbance of digestive functions

The retardation, or in some cases even the cessation, of digestive processes in the poisoned animals is not wholly understood. Casper (1859) observed that in post-mortem examinations of animals poisoned by nitrobenzene the stomach contents were always alkaline; and, since the acidity of the fluid in the stomach, especially in the pyloric end, has been shown to be essential to gastric digestion (Howell, 1918), it is possible that nitrobenzene in some way hinders the formation or secretion of hydrochloric acid.

Cerebellar disturbances

Turning now to the evidence indicating cerebellar involvement, the following facts may be noted. From the descriptions it will be seen, as already stated, that there is scarcely a single one of the symptoms appearing in cases of nitrobenzene poisoning that cannot be referred to disturbances in the cerebellum or the cerebellar paths, barring those which are undoubtedly due to a direct action on the blood. Moreover, this conclusion appears to be borne out by histological data, since the cerebellum is the only organ in which definite histological changes were found.

Nausea and vomiting.— Nausea and vomiting, accompanied by some of the symptoms named above, may be due to disorders of the cerebellar paths (Jelliffe, 1913). Nausea and vomiting may appear during the fumigation process, altho the animal may show no other pronounced symptoms for several days; but this does not preclude the possibility that nausea and vomiting are the result of the action of nitrobenzene on the cerebellum, since it is possible that a sufficient amount of the drug may be concentrated in the cerebellum to cause these first symptoms without enough being present to produce any further symptoms; moreover, if the animal were left in the fumigation chamber for a little longer period, the other symptoms would appear very quickly. If the cause of the vomiting were to be ascribed to a peripheral action of the drug, then the same explanation would have to be given as for the cause of the vomiting after the latent period, it would seem.

Ataxia.— The type of motor ataxia exhibited by animals poisoned by nitrobenzene, especially by dogs and birds, is typically cerebellar.

This is indicated by the hobble or sprawling gait in walking, the position of the legs in standing, and other characteristics mentioned heretofore (page 462).

Adiadochokinesis.— Adiadochokinesis is, perhaps, the best interpretation of the type of convulsions observed. This is a term originally used by Babinski to describe a peculiar type of incoordination in patients (Jelliffe, 1913). It is seen in the absence of paralysis, muscle palsies, and sensibility disturbances, and is characterized by a loss of ability to carry out rapidly alternating movements, such as flexion and extension of the forearm on the arm. In dogs, birds, rats, and other animals poisoned by nitrobenzene, it was observed that at times one set of muscles would be contracted and another set relaxed, and at other times just the reverse happened. For example, if motor impulses passed to the extensors of the hind legs, the animal was unable to stop these impulses or to use the antagonistic muscles, and the leg remained for a time rigidly extended; again, if the impulses passed to the flexors, then the animal was unable to extend the leg. This condition, according to Babinski, indicates involvement of the cerebellar paths.

Nystagmus.— According to Jelliffe (1913), Holmes states that "nystagmus is a common and very valuable localizing sign of local cerebellar lesions. It is almost certainly a true cerebellar symptom." Nystagmus does not always appear, but when present it is invariably a cerebellar type, distinguishable from vestibular nystagmus by the jerky movements of the eyeball. The shifting is in a lateral plane, and is equally rapid in either direction.

Asthenia.— Asthenia is one of the first symptoms to appear and is almost invariably present. The animal is usually so weak that when it is placed on its feet, its legs literally double up beneath it, and its head sways about as if the neck were disjointed. This symptom, according to Jelliffe (1913), indicates "disorder of the tractus cerebellovestibularis spinalis, or rubro-spinalis."

Hypotonus.— Hypotonus, as revealed by palpation of the muscles and by special tests of the tendon reflexes, was observed in the more advanced cases, especially, of nitrobenzene poisoning. In some cases this symptom was accompanied by poor tendon reflex reactions, while in other cases the tendon reflexes were normal or even exaggerated. These conditions indicate cerebellar hypotonus.

Disturbance of respiration.— In moribund animals poisoned by nitrobenzene, one almost invariably observes a disturbance of respiration, and in some instances a slowing of the pulse rate. Musser (1904) states that cerebellar tumors often cause symptoms of this type.

Headache and tenderness of the occiput.— Headache in animals is very difficult, if not entirely impossible, to determine. However, certain actions exhibited by animals poisoned by nitrobenzene might be interpreted to indicate headache; for instance, the animal's desire to press its head against some object. Dog I was observed to stand for long intervals with its head pressed against the attendant's legs or against some solid object (page 431). And certainly the fact that the animal exhibited some discomfort if the back of its head was touched, indicated a tenderness in the vicinity of the occiput. These symptoms have been observed in cases of cerebellar tumors.

Circus movements.— Rotation of the head and the neck was always observed in the case of birds poisoned by nitrobenzene. This is a characteristic symptom observed in cerebellar pigeons. Rotation of the body about its longitudinal axis, observed especially in gray rats and sometimes in dogs, is a symptom exhibited in cerebellar mammals.

CAUSE OF THE LATENT PERIOD

The fact that there often exists a long latent period, the period of time elapsing between the administration of the drug and the onset of the symptoms, has led to much theorizing as to its cause. The following two theories have been the most popular: the theory advanced by Ollivier and Bergeron and held to by Letheby, that nitrobenzene is converted into anilin in the body and that time is required for this transformation; and the theory investigated first by Filehne and accepted by most recent writers, that the drug is so lightly soluble in the tissues of the body that time is required for the absorption of it in sufficient amounts to produce the poisonous effects.

Filehne has ably shown that the action of the drug does not depend on its conversion into other chemicals. Furthermore, he failed to find any trace of anilin in any of the organs of animals poisoned by nitrobenzene even by the hypochlorite test. His criticism of the isophenylcyanide test (used by Letheby) is justified, since in conducting this test nitrobenzene

is itself converted into anilin. Filehne has shown also that the theory of slow absorption does not account for the rapid action of the drug observed in certain cases.

In all probability the rate of absorption of nitrobenzene by the body tissues does have something to do with the cause of the latent period; but the explanation must be primarily based on the readiness with which the drug is absorbed by certain tissues as compared with other tissues, and not alone on the rate of absorption by the tissues in general. It will be recalled that nitrobenzene is readily soluble in oils and the liquid fats; it is soluble also to a certain extent in lipoids, but probably to a less extent in certain lipoids than in others, and even the same lipoid may absorb the drug more readily under certain conditions than under other conditions.

When the drug is administered by vapor inhalation, the amount absorbed by the blood (at a given vapor pressure) depends, undoubtedly, on the amount and the condition of the fats or the lipoids in the blood. Also, the amount absorbed from the blood and held in solution by the body fats is, in all probability, directly proportional to the absorption power of the body fats over the absorption power of the fats in the blood.

Since nitrobenzene is more readily absorbed by the liquid body-fats than by the lipoids (of the brain), large amounts of it may be stored in the liquid fats of the body without the animal's showing any immediate symptoms of poisoning. Moreover, since the action of the drug on the cells of the brain probably depends on its concentration in the vicinity of these cells — as in the case of chloroform, ether, and other drugs that act directly on the cells of the brain — nitrobenzene, depending on the amount and the condition of the lipoids and the fats held in suspension in the blood, may be picked up from the body fats by the blood in such small amounts as to be in time entirely eliminated from the body without ever giving a sufficient concentration in the vicinity of Purkinje's cells to cause symptoms of poisoning; so that large amounts of the drug may be stored in the body without the animal's ever showing any symptom of poisoning.

On the other hand, depending on the concentration of nitrobenzene in the blood supply to the cerebellum, a sufficient concentration of the drug in the vicinity of the Purkinje cells might be reached, even after minute

doses, to affect these cells and produce the typical symptoms of poisoning, or even death, within a very short time after the administering of the poison.

If the above assumptions are correct — and they can be so proved only after a long series of experiments dealing more exhaustively with the physics, chemistry, and physiology of the subject — then it is not surprising that, as was found, the latent period, as well as the intensity of the action of the drug, should vary in different individual animals, or even in the same individual at different periods of time; for neither the amount nor the kind of fats in the blood or the nervous tissues is absolutely constant.

CONCLUSIONS

The present work has confirmed the findings of previous investigators regarding all six of the points listed in the first paragraph following the review of the literature. In addition the following conclusions have been deduced:

1. Aside from the possible disturbance of digestive functions and a possible asphyxia due to a direct action of nitrobenzene on the blood, most, if not all, of the observed symptoms of nitrobenzene poisoning may be explained on the basis of disturbances in the cerebellum or the cerebellar paths.

2. Toxic doses of nitrobenzene, when administered by vapor inhalation, exert a direct action on the Purkinje cells in the cerebellum, causing chromatolytic degeneration of these cells.

3. Histological examinations have failed to reveal any definite changes in any of the organs of the body except the blood (presence of methemoglobin and morphological alterations of erythrocytes) and the cerebellum (chromatolytic degeneration of the Purkinje cells).[13]

4. The size of the lethal dose probably depends on conditions such as the amount and the kind of fats in the blood, which favor or disfavor a concentration of the drug in the vicinity of the nerve cells.

5. The latent period (the time elapsing between the administration of the poison and the onset of the symptoms) is undoubtedly due to the

[13] The writer does not mean to assert that histological changes do not occur in other tissues, especially in other parts of the central nervous system. Indeed, a further study of the present sections may yet reveal such changes. It would be strange if the action of nitrobenzene on the central nervous system were confined to a single type of cells only. Probably in cases of fatal poisoning other nerve cells are involved also, but it will be difficult to determine whether such changes are due to a direct action of the poison or are the result of a complication of changes attending death by poisoning. Further investigations are being made along this line.

absorption of the nitrobenzene from the blood, and its retention by the liquid fats of the body in which it is easily soluble. As the concentration of the poison in the blood lipoids and fats diminishes, in relation to its concentration in the body fats, the nitrobenzene is given up again to the blood; and in the course of time, a sufficient concentration of the poison in the lipoids of the cerebellar or other brain cells is reached to produce an onset of the motor symptoms. The time required to bring this about (the latent period) depends on the same factors as those on which the size of the lethal dose depends, and is undoubtedly hastened by the ingestion of solvents of nitrobenzene, such as alcohols, fats, oils, milk, and the like. Possibly, also, the condition of the brain lipoids at a given time may be an important factor in hastening or retarding the absorption of nitrobenzene by these lipoids.

6. Nitrobenzene cannot be used, with any degree of safety, for the fumigation of animals to destroy their external parasites. The lethal dose for birds and mammals is rather variable but it may be very small; and from these experiments it will be seen that apparently a shorter period of fumigation at a given temperature is required in order to kill a domestic animal than to kill even a fair proportion of either fleas or biting lice. However, as has been pointed out by the writer in a previous paper (Chandler, 1917), the drug may be used, with the exercise of caution, for collecting external parasites from animals, by fumigating the animals at low temperatures and for short periods of time — at a temperature not over 20° C., and for a period not longer than one and one-half hours. Under these conditions the parasites may be stupefied without any appreciable damage being done to the host; but the drug is dangerous to handle under any conditions.

7. Because of the extreme toxic properties and the subtle action of nitrobenzene, the following uses of this drug should be prohibited by legislation: for perfuming soaps, lotions, and pomades; as a solvent in shoe polish, floor wax, and the like; and especially as an ingredient of flavoring extracts, confections, and liqueurs. The drug should be regarded as one of the most dangerous of poisons, and its sale and use should be regulated by law just as in the case of any other deadly poison.

8. Nitrobenzene should be given serious consideration as an industrial poison. Munition plants, dye works, and other factories which handle

nitrobenzene, should be inspected with the view of installing devices to prevent workmen from inhaling the vapor or coming into contact with the liquid.

9. In view of the evident relation existing between the lethal dose of nitrobenzene and the amount and kind of fats and other solvents of the drug present in the blood, it would appear highly desirable that further investigations should be undertaken with the view of working out rational therapeutics for cases of poisoning.

10. Since the findings in these experiments indicate that the symptoms of nitrobenzene poisoning are caused by a direct action of the drug on the Purkinje cells, causing these cells to degenerate, and since different sets of muscles appear to be involved at different times, it would appear that further investigations might be of value from the standpoint of obtaining more exact data regarding the localization of functions in the cerebellum.

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CONTENTS

STUDIES IN THE REVERSIBILITY OF THE COLLOIDAL CONDITION OF SOILS

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A. B. Beaumont

The early workers in the field of colloid chemistry considered substances possessing colloidal properties to be distinct chemical individuals. Those working with soil problems spoke of certain inorganic and organic colloids. The colloids found, and thought to exist, in the soil were few in number. Colloidal silica, alumina, and ferric oxide among the inorganic compounds, and the various organic substances commonly designated as humus, are the most frequently mentioned in the literature. Additions have been made to this list from time to time, and occasionally sharp controversies have arisen as to whether the substance in question exists in the soil as a crystalloid or as a colloid. The contradictory results in many cases probably can be accounted for by the different geological conditions under which the soils studied have been formed.

The modern conception, as expressed by leading writers on the subject, is that colloids are to be considered as a state or condition of matter, not as chemical individuals. It has, of course, been long recognized that some few substances — for example, silica — exist both as crystalloids and as colloids. But recent investigations of Von Weimarn and others have so increased the number of substances that have been prepared in the colloidal conditions, as to lead some to believe that nearly all substances can exist as colloids as well as crystalloids; and Von Weimarn (quoted by Ostwald, 1915 : 101) has gone so far as to proclaim that "the colloid, like the crystalloid, is a universally possible state of matter."

It was in accordance with this modern conception of colloidality that the work herein described was undertaken, and the data presented show that the colloidal condition of the soils worked with is dependent, in a degree at least, upon circumstances and environment. The object of the work undertaken was to throw some light on the physical changes, and their effects, which a soil undergoes with variations in its moisture content, especially on being wetted and dried. As is shown later, the prob-

lem has been attacked in many ways previously. It was thought well to attack it from the standpoint and with the methods of colloid chemistry. It has resolved itself into a study of the reversibility of the colloidal condition of soils.

REVERSIBILITY DEFINED

Several different meanings have been attached to the word *reversibility*. According to Ostwald (1915 : 40), "when a change in the state of a colloid may be reversed by reversing the conditions which brought that change about, it is said to be 'reversible.'" The word is commonly applied to the change between the sol and gel conditions. Thus, if a colloid which has been precipitated by a salt goes back into solution on removal of the salt by washing, the colloid change is said to be reversible; if this does not occur, the colloid change is irreversible.

Ostwald states that the reversibility of a change is not determined, in the main, by the nature of the colloid itself, but by the character of the conditions that produce the coagulation. For instance, the precipitation of the typical protein sols by neutral salts is reversible, whereas their precipitation by heat is irreversible. Ostwald states that one cannot, therefore, properly speak of reversible and irreversible colloids, but only of reversible and irreversible changes.

Zsigmondy (Zsigmondy and Spear, 1917) divides colloids into reversible and irreversible, depending on whether or not they leave a soluble residue on evaporation. The irreversible colloids he still further divides into two groups: to the first class belong those that coagulate in dilute solution and precipitate in the form of a powder rather than as jelly; the second class consists of those that may be considerably concentrated before coagulation sets in, and whose precipitates are decidedly jelly-like, such as colloidal silicic acid, clay, and ferric oxide. The colloids of the first group are considered completely irreversible. Those of the second group, which includes some most commonly found in the soil, can, on the other hand, be brought back to the hydrosol state by the addition of a small quantity of a suitable reagent, provided the residue has not been too thoroly dehydrated.

Typical reversible colloids, after sufficient swelling has occurred, dissolve in a solvent to give a homogeneous-appearing solution. Gum arabic, albumin, and ordinary glue are good examples.

The meaning of the word *reversibility* as above interpreted is too narrow when applied to soils. Ehrenberg (1915) states that the meaning is not so much erroneous as of too little extension. In dealing with soils from the agricultural standpoint the cases in which a hydrosol is possible are the exception, not the rule. Such cases would be the flooding of rice fields, cranberry bogs, and other soils the crops or the culture of which require an excess of water at times. Reversibility of soil colloids in the narrow sense above described would be of more or less importance in the case of a temporary excess of water, as in rains and in the application of irrigation waters, especially by the flooding methods. From the standpoint of the geological formation of alluvial, lacustrine, and marine soils, this sort of reversibility would be of considerable importance.

However, in considering the reversibility of the colloidal state of the great masses of agricultural soils, one's concern is more with the change from the gel to the non-gel form and vice versa. The reversibility studies of Van Bemmelen with various oxides dealt with the gel and non-gel forms, and the word *reversibility* is used by some writers in referring to those changes. It is a word which is convenient to use and is expressive.

In a consideration of the reversibility of the colloidal condition of soils, it seems that the indirect cases which occur thru chemical and biological actions should be included, such as the hydration of iron salts, the action of bacteria, and the growth of lower forms of plant life. It will be seen in the presentation of results that some of these actions are considerably affected by changes in the moisture content of the soil. Reversibility of the colloidal state of soils should include, therefore, all cases brought about by physical, chemical, and biological agencies or a combination of these. In fact, most of the changes of the colloidal states of soils are probably due to a combination of forces. These changes may be represented as follows:

$$\text{Non-colloidal state} \rightleftarrows \text{Colloidal state} \begin{cases} \text{Sol} \\ \uparrow\downarrow \\ \text{Gel} \end{cases}$$

COLLOIDAL MATERIALS IN SOILS

Way (1854) reported deposits of soluble or gelatinous silica in the lower beds of the chalk formation. The silica, soluble in alkalies, in the samples examined ranged from 5 to 72 per cent.

Schloesing (1874) was one of the first to call attention to the colloidal matter of soils. From a clay he isolated a gelatinous mass which consisted mainly of water, silica, and alumina, with small quantities of ferric oxide, magnesia, and potassa.

Van Bemmelen (1888) attributed the absorptive properties of soils largely to the colloidal matter which he believed to surround most particles of soils. This matter consists of ferric oxide, silica, silicates, and organic matter in various stages of decomposition. These materials unite with one another or with other substances to form what Van Bemmelen designated as *adsorption compounds*.

Warington (1900) claimed that true colloidal clay is always an aluminum silicate, but also mentioned the presence in some soils of ferric oxide, hydrated alumina, and colloidal humus.

Schloesing (1901) states that colloidal alumina occurs in European soils in very small quantities, but he found very much free alumina in soil samples from Madagascar. This results from the weathering of silicates and later hydrolysis, as in the case of colloidal ferric oxide. Hilgard (1911) inclines to a similar view, and sees in the presence of gibbsite and bauxite a reason for the assumption of the free alumina in soils.

Cameron and Bell (1905) dispute the presence of colloidal alumina in normal soils. Lacroix (1914) reports it in the decomposition products of aluminum silicates, and McGeorge (1916) reports having found it in the soils of Hawaii.

Ries (1908) includes among the ingredients of clay that may assume a colloidal form, aluminum hydroxide, iron hydroxide, hydrated silicic acid, and organic matter.

Hilgard (1911) considers that colloidal clay is clay which will remain suspended in a column of water eight inches high during twenty-four hours, and that the nature of this colloidal clay varies considerably in composition. According to this author, colloidal clay contains ferric hydrate and other colloidal, or at least amorphous, substances such as silicic, aluminic, and zeolitic hydrates.

Gans (1913) and Wiegner (1912) carried on an extended controversy as to whether an artificially prepared colloidal silicate was a chemical compound or a mixture of gels. Wiegner was of the opinion that it was a mixture of gels, and that owing to its similarity to the natural soil zeolites

they also are mixtures of colloidal gels. Gans thought that the substance was a chemical compound, but admitted the possibility of its existing in the colloidal state.

Ehrenberg (1915) classifies soil colloids broadly into systems based on the physical condition of their phases. Colloidal silica and humus are placed in the liquid-liquid system, and the colloidal ferric oxide and alumina in the solid-liquid system.

Colloidal silica originates from the remains of plants and from the weathering of rocks. The final state may be colloidal or crystalloidal, depending on the speed of the reaction. If the change is rapid, a colloid such as opal may be formed; while if it is slow, quartz crystals are formed.

Iron compounds occur in soils in relatively large quantities and widely distributed. If these become dissolved in water, colloidal ferric oxide easily forms by hydrolysis under ordinary conditions. With difficultly soluble iron compounds such as silicates, weathering and consequent solution are necessary.

Microscopic plant and animal life are colloidal. Altho bacteria may be present in large numbers, because of their comparatively small mass they are not very important as compared with other soil colloids.

Colloidal humus originates from all sorts of plant and animal remains, is not chemically defined, and varies in all degrees between solid and liquid. It stands on the boundary line between a colloidal and a crystalloidal condition, as shown by a slight dialyzability and conductivity.

Spear (Zsigmondy and Spear, 1917) states that colloidal silica, silicates, hydroxides of iron, aluminum, and manganese, and colloidal matter such as humus, exist in the soil.

From what has been said so far it is evident that a great many materials existing in the soil in the colloidal condition have been identified and studied. There is little doubt (Ehrenberg, 1915) that many other substances exist in the soil in this condition, and that, as methods of colloid chemistry are further developed and the range of soils examined is extended, additions will be made to the list. It is possible that every soil constituent will be found to exist in the colloidal condition under some circumstances.

Methods for determining the amounts of colloids in soils have not been sufficiently developed to enable one to determine these amounts with any great degree of accuracy. At best, the measurement is only an estimation. Evidence of the unsatisfactory status of methods exists in the

great number that have been evolved from time to time and used with varying success by different investigators.

There is little doubt that the amounts of colloids in soils vary considerably with the kind of soil and the conditions. Schloesing (quoted by Ehrenberg, 1915) estimated that the colloidal clay of normal agricultural soils seldom exceeds 1.5 per cent. However, he found as much as 35 per cent of colloidal matter in extremely heavy soils.

Hilgard (1911) estimated the amounts of colloidal clay in soils as varying from 0.5 per cent for very sandy soils to 45 per cent and over for heavy clay soils.

Tempany (1917) calculated the amounts of colloidal matter in soils from their linear shrinkage on drying, and gives figures varying from 9 to 64 per cent.

REVIEW OF LITERATURE

It has been observed by many investigators that for some soils previous drying is beneficial from the standpoint of plant production. This benefit has been ascribed by some writers to the effect on the physical condition of the soil. Alternate wetting and drying has been considered particularly efficacious in this respect. Of late the effect on the colloidal matter in particular has become a favorite assumption of some writers. In other cases the benefits of drying or of alternate drying and wetting are attributed to chemical or biological effects, or to a combination of these with physical effects. On this point Lyon, Fippin, and Buckman (1915 : 188) say: "Just what may be the effects of wetting and drying on the colloidal matter of soil is a question."

The increased productiveness of soils due to fallowing is also a matter of common experience. The stirring of the soil is accompanied by rapid drying. To what extent the benefits are due to physical, chemical, or biological effects, has not been worked out.

Buckman (1911) concluded from the work of others that under conditions of extreme dryness an increase in moisture means an increase in nitrates. Lyon and Bizzell (1913) found that an increase in moisture after a dry period was sometimes accompanied by an increase in nitrates in an unplanted soil, and Lyon (1907) expressed the opinion that a dry period previous to the time of heading causes wheat to be harder and higher in protein.

The beneficial effects on fertility from burning the soil have long been known. In Europe and England the practice of burning, and of paring and burning, the soils was very common at one time. It has been thought by many that the beneficial effects of this practice were due to a physical bettering of the soil (King, 1906).

It has been observed in India (Howard and Howard, 1910) that the drying of the alluvial soils in direct sunlight increases their productivity, and some of the natives make a practice of exposing their soils to this ameliorating influence.

According to Alway and Vail (1909), the moistening and drying-out of soils under some conditions causes a natural fertilization of the deeper layers due to the falling of the organic matter into the cracks.

Ehrenberg (1915) states that many investigators have observed a bettering of the quality of the soil as a result of its drying out, and quotes Vanha as saying that the energetic drying-out of soils rich in humus favors the quality of such soils especially.

In connection with the benefits of drying soils, Ehrenberg cites the old custom of using garden walls made of loam as a fertilizer; and King (1911) tells of the practice among the Chinese of tearing out "kangs" that have been made of clay subsoil and thoroly dried, and using them as fertilizer.

Ehrenberg is of the opinion that only soils containing considerable organic matter are affected by drying. The effects of drying upon other soils are very slight indeed, and are quickly lost on the soil's being wetted, according to that author.

The effects of drying the soil are sometimes injurious. Hilgard (1911) reports injuries to plants caused by the drying and cracking of soils and the consequent mechanical tearing of the root systems. Sometimes the shrinking of the surface crust of soil around the stems of grain causes a constriction that is injurious. Ehrenberg has reported that a disease of sugar beets is traceable to such mechanical injury.

Mathews (1916) has pointed out the importance of moisture conditions in the irrigation of certain heavy soils. If the surface of these soils has been dried and then wetted, the irrigation water enters slowly, due to the swelling of the soil and the closing of the cracks.

The extensive literature bearing on the specific physical, chemical, and biological effects of moisture changes in soils has been rather fully sum-

marized by Cameron and Gallagher (1908), Lyon and Bizzell (1910), Kelley and McGeorge (1913), and Klein (1915).

Cameron and Gallagher show a variation in the volume of soils with repeated wetting and drying, depending on the previous condition of the soil. Finally a condition of natural packing is reached, at which the expansion on wetting is equal to the contraction on drying.

Lyon and Bizzell found, along with other investigators, that the effect of steam sterilization was to increase the soluble matter of both organic and inorganic constituents. This increase was particularly marked in the case of organic matter.

Kelley and McGeorge studied the water and acid extracts of different soils that had been air-dried and others that had been dried at higher temperatures. They found that on an average the solubility of the constituents increased with the temperature of drying. Iron was an exception. The high solubility of the soils used in aquatic agriculture is, according to these investigators, decreased by drying. They say the subject is very complex, and among the many factors involved are flocculation of colloids, oxidation, deoxidation, decomposition, dehydration, and the attending physical alterations of the soil film.

Klein's work is divided into two parts. In experiment 1, the effect of partial drying of soils on total water-soluble salts, nitrates, potassium, calcium, and acid-soluble phosphorus, and on the growth of plants, is studied. In experiment 2, the effect of complete air-drying on the production of carbon dioxide and nitrates is studied. In this experiment the soils were repeatedly wetted and dried, three dryings being the maximum. Klein arrived at the following conclusions, among others:

In experiment 1: (1) Drying the soil previous to planting has a beneficial effect on plant growth. (2) The water-soluble matter is increased by drying in a soil low in organic matter, but is decreased in a soil high in organic matter. (3) Drying the soil has but little effect on the available potassium, calcium, and phosphorus of the soil.

In experiment 2: (1) Bacterial activity, as measured by carbon-dioxide production, is increased by a previous drying of the soil. (2) Previous drying increases the soil nitrification, reaching a maximum with three dryings. The author thinks that the physical effects of drying are important in this connection, and that the flocculation of the colloidal material is very important.

Christensen (1917) states as a result of his studies that the ability of soils to free acid from calcium-acetate solution is from two to four times as great in the air-dry as in the moist condition, a result just the opposite of what was expected. With litmus solution and litmus paper, however, practically no difference was noticeable as a result of drying.

The classical and fundamental researches of Van Bemmelen (1909) on the reversibility of the hydrogels of various oxides have supplied the greater part of the knowledge on this subject. He worked particularly with the hydrogel of silica. By placing the hydrogel in desiccators, each with a different vapor pressure, he obtained data which showed that the final dehydration depends on the preparation and previous history of the gel and on the vapor pressure at a given temperature. It was found that by lowering and raising the vapor pressure, within certain limits, dehydration and rehydration are possible repeatedly, altho the reversibility is not always along the same path or complete. In other words, unless dehydrated too far the dried gel eagerly took up water again, but did not take up as much as it previously had nor did the volume return to its original size.

According to Cushman (1904), if the hydrogel of silica is heated to a temperature of about 1000° C. it loses its power to take up moisture to any great extent. However, a small amount of moisture is taken up.

Van Bemmelen worked also with colloidal oxides of alumina, iron, and other metals. For ferric oxide and alumina he found results similar to those for silica but with minor differences in regard to transition points.

Zsigmondy (Zsigmondy and Spear, 1917) points out that irreversible colloids may become reversible by the addition of reversible colloids. This is probably an adsorption phenomenon, and opens up interesting possibilities because of the lack of uniformity in the composition of soils.

Muller (1907) prepared a reversible colloidal alumina by peptizing a freshly precipitated aluminum hydroxide with hydrochloric acid. The hydrosol thus obtained is fairly stable, and leaves a precipitate which is soluble in water.

Ehrenberg (1915) reports Schloesing as saying that an artificial clay may be made by mixing 1 per cent of glue with finely pulverized sand. This mixture exhibits reversibility of properties, cohesion, and plasticity, on being dried and wetted.

Hilgard (1911) observed that his "colloidal clay," which could be obtained from a suspension either by evaporation or by flocculation, exhibited reversibility. When it dried it shrank as so much boiled starch, and on being remoistened it swelled quickly, resuming its former jelly-like consistency. Moistened with less water it became highly plastic and adhesive.

Grout (1906), in attempting to raise the plasticity of clays, found that agar-agar mixed with clay was effective but alumina cream was less effective. Furthermore, after being air-dried, powdered, and mixed, the plasticity of the alumina cream as used was irreversible. Grout also prepared an artificial hydrated silicate of alumina, and found that this also was irreversible after drying.

Ashley (1909), in commenting on Grout's work, said it seemed to Grout that none of these or other colloids could be responsible for the behavior of natural clays; for he apparently thought that clay could be dried and wetted repeatedly without injuriously affecting its plasticity, or, in other words, without affecting the activity of the colloids. Ashley said further that in this supposition Grout was not in accord with practical experience. Clay used by potters has in most cases never been deprived of its natural moisture. After once being dried out at as low a temperature as 60° C., it is found to have lost noticeably in plasticity.

Ehrenberg (1915) cites the work of Thaer and Ostwald, and states that it can be said with a considerable degree of certainty that humus is reversible. How far humus is affected by aging is not known. The study of it is restricted by its not having a definite chemical composition.

Little is known concerning the behavior of humus gel, according to Ehrenberg, but he states that according to Zailer and Wilk humus gel does not suffer many changes in drying out; that it exhibits simple swelling phenomena, but does not come back to its original volume if it is more or less dried. To substantiate this point he cites data from Wollny showing that the greater the depth at which dried peat was taken, the more it increased in volume on being moistened. The surface layers, having been dried the more, increased less.

Warington (1900) cites Schloesing's experiment in which he mixed calcium humate with clay and found that the humate had considerable cementing power, which it lost on being dried. The irreversible character here is probably due to the absorption of the calcium in the preparation

of the humate. Humus gel made by evaporating the sol, as ordinarily prepared, is reversible.

Rohland (1914) reports that the adsorptive power of soil colloids for water decreases after repeated drying, but that new colloids are formed by clays standing in an excess of water.

According to Ehrenberg (1915), Schubler reported that a humus colloid prepared by him could not take up as much water after drying out as before. Wiegmann confirmed this statement. A similar observation was made by Schubler on a strongly humus-containing soil. Lasius reported that peat once dried does not soften again, and Ruhlmann stated that peat when once air-dried cannot be brought back to its original slimy condition thru working.

Tacke and Immendorff (1898) report that peaty soils not only shrink strongly by natural or artificial drying, but that they lose their swelling capacity, take on a peculiar sandy condition, and never again become strongly colloidal. Further, these investigators report that the solubility of phosphoric acid in moor soil is increased by drying the soil at about 80° C. They also found an increase in the water-soluble potassium and calcium, due to drying out. This effect was masked by using 0.5-percent hydrochloric acid as a solvent.

Mitscherlich (1902), working with moor soil, found that moistening and then drying at 100° C. affects the soil structure so that it holds less water. He concludes that moistening and drying a soil is not a simple reversible process.

The destruction of the crumb structure of soil in good tilth by the beating of rains has been recorded by several writers, including Warington, Hilgard, and Ehrenberg. This is a case of deflocculation brought about by physical agencies.

Harrison (1917) reports that wet methods of cultivation when first applied to paddy soils tend to bring about a physical deflocculation followed by a weathering of particles, thus causing the soils to become heavier. This heaviness is probably due to a production of the colloidal condition.

Tempany (1917), in studying the shrinkage of the soils of the West Indies, assumes that the gel condition of the colloidal matter in these soils is restored by moistening and kneading the air-dry soil — a case of physical reversibility, largely.

In ceramics the practice of increasing or bringing back the plasticity of clays by keeping them soaked with water for several months is a common one. The effect of this aging as well as weathering may be the production of the colloidal condition by hydrolysis, according to Ries (1908). Mechanical grinding is often as efficacious as aging in improving plasticity. In this connection Rohland (1911) says: "By repeated moistening with water the amount of colloids is increased and thereby plasticity is raised."

Ruprecht and Morse (1917) show the positive presence of soluble salts of iron, aluminum, and manganese in soils long treated with ammonium sulfate, and it is to these soluble salts that toxicity is ascribed. Morse and Curry (1908) show that the presence of calcium carbonate prevents the formation of soluble iron and aluminum salts in soils treated with certain solutions.

The soil from limed plats shows a greater adsorption for dyes than does that from unlimed plats (Ruprecht and Morse, 1915). This indicates more colloidal matter due to the liming. As pointed out by Ruprecht and Morse, this is probably due to a flocculation or a precipitation of the iron and aluminum in some form by the calcium compounds. If so, this presents a case of chemical reversibility which is of importance as regards the toxic effect of ammonium sulfate long used as fertilizer.

In the formation of iron-pan in moor soils, as cited by Warington (1900), a similar case of chemical reversibility of the colloidal condition is presented. The iron passes into the soil as soluble salts and is later precipitated as colloidal ferric oxide. Under certain conditions this may again go into solution and the process be repeated.

Summary of literature cited

While the observations and the results of investigations that have been mentioned are more or less conflicting, it seems that the following points stand out:

1. Previous drying of a soil is, in general, favorable to its fertility.
2. Data have been obtained which show that this effect on fertility may be traced to physical, chemical, and biological causes.
3. Drying and wetting some soils produces volume changes, and affects the water-holding capacity, the penetrability, and other physical properties.

4. Alternate drying and wetting of some soils favors some of the soil activities which are correlated with fertility.

5. Previous drying increases the solubility of inorganic and organic constituents, such increase usually accompanying an increase in the temperature of drying.

6. Soils containing considerable organic matter are affected by moisture changes to a greater degree than are those containing small amounts of organic matter.

7. Changes in certain physical properties of soils, such as cohesion and plasticity, are, to a degree at least, reversed by moisture changes.

8. Changes in the properties of soils due to moisture changes have been attributed by many workers to changes in the colloidal condition.

9. Studies with more or less pure colloidal materials usually found in the soil in the colloidal condition indicate a possible reversibility of all these materials under some conditions.

10. Most of these studies cited have been on soil properties other than colloidal, and with methods other than those of colloid chemistry.

EXPERIMENTAL WORK

Study of methods

Snyder (1917) lists eighteen possible methods, under eight distinct headings, for measuring the colloidal content of soils. The relative merits of some of these have been discussed fully by Stremme and Aarnio (1911), and Snyder reviews all of them.

Altho most writers on the subject are of the opinion that the method of water-vapor adsorption, originally devised by Mitscherlich (1905), is the best general method for measuring colloidal content, Snyder thinks that the dye-adsorption method, first used by Ashley (1909), has the greatest possibilities. Snyder recognizes the specificity of dyes for particular colloids. These two methods are undoubtedly the most feasible and practicable at present known.

Owing to the unsatisfactory status of methods for measuring colloidality, it was felt necessary to investigate some points most commonly disputed. Also, in the attempt to use various methods, some difficulties were encountered which required settling. Some time was spent, therefore, in preliminary work on methods before they were worked out as

finally used. As some of the data obtained may be of interest, they are here presented.

Effect of temperature on adsorption of water vapor.— The effect of temperature on adsorption of water vapor is a point that has been disputed. Patten and Gallagher (1908) and some other investigators (Taylor, 1915) have found a decrease in adsorption with an increase of temperature. This is what one would expect from a consideration of Le Chatelier's theorem, for adsorption is accompanied by a liberation of heat, a rise in temperature. Therefore, raising the temperature would tend to reduce adsorption rather than to increase it.

Hilgard (1911), Lipman and Sharp (1911), and recently Alway, Klein, and McDole (1917), on the other hand, think that the amount of water vapor adsorbed increases with the rise in temperature. The experimental work of hygroscopicity determinations has a high probable error. This should be taken into consideration in drawing conclusions from the data, which was not done by any of these investigators.

In order to learn whether any great differences were obtainable with slight variations in temperature, adsorptions were run at various temperatures. The results are given in table 1. The results show differences, but in no case is the difference sufficiently greater than its probable error [1]

TABLE 1. EFFECT OF TEMPERATURE CHANGES ON THE ADSORPTION OF WATER VAPOR BY DUNKIRK SURFACE SOIL

	Per cent* of water vapor adsorbed	Difference
At 15° C	3.450±0.055	
		0.175±0.066
At 20° C	3.275±0.037	
		0.095±0.066
At 30° C	3.180±0.055	
		0.150±0.097
At 40° C	3.330±0.080	

* Unless otherwise stated, all percentage calculations in this article are based on oven-dried weights of soil.

[1] The probable error of the mean in this and all other experiments cited in this article was calculated by means of Peter's approximation formula, given by Mellor (1913). The probable error of the mean is $\frac{0.8453 \sum (+v)}{n\sqrt{(n-1)}}$, in which $\sum (+v)$ is the sum of the deviations of all the individuals from the mean, without regard to the sign, and n is the number of individuals. If the difference between means is 3.8 times its probable error, the chance is 30 to 1 (Wood and Stratton, 1910) that the difference is significant.

to justify the drawing of the conclusion that temperature variations of from 5 to 10 degrees, within the limits of the experiment, make an appreciable difference in the amount of water vapor adsorbed.

These data, being limited, are not to be taken as conclusive as regards the question. It was thought justifiable, however, to disregard slight variations in temperature and to run all tests at room temperature. In order to reduce the fluctuations in temperature, the apparatus was put into a thick-walled, insulated, wooden box.

Water-vapor-adsorption method not equally applicable to all soils.— Originally it was intended to use in the experiments a glacial clay subsoil of the Dunkirk series. The sample used was taken from an excavation at a depth of about eight feet. The soil was placed in a humidifier, along with surface soil of the same series but from a different locality. In this particular experiment, saturated strips of heavy cardboard were used instead of the cotton cloth mentioned later in connection with other experiments. The results of this experiment are given in table 2. A gradual increase in the amount of water vapor adsorbed by the subsoil

TABLE 2. ADSORPTION OF WATER VAPOR BY A NORMAL (DUNKIRK SURFACE) AND AN ABNORMAL (GLACIAL SUBSOIL) SOIL

Time exposed	Per cent of water vapor adsorbed by			
	Dunkirk surface soil		Glacial subsoil	
	Dry	Moist	Dry	Moist
7 days	3.38	4.35	27.25	30.7
12 days	3.50	4.27	38.90	40.6
17 days	3.75	4.45	48.70	52.4
24 days	3.47	4.23	57.00	61.2

may be noted, free water being present after seven days; whereas the surface soil showed no more variation in the amount adsorbed than could be ascribed to experimental error.

These results show a weakness in the water-vapor-adsorption method, namely, that some soils adsorb an abnormal amount of water vapor and therefore cannot be used in such experimentation.

The unusual adsorption appears to be due to the chemical rather than to the physical condition of the soil, and is therefore, properly speaking,

absorption. The subsoil was known to contain large quantities of soluble salts, among which were calcium magnesium and chlorine ions. As a consequence of this irregularity, this subsoil was eliminated from the tests of water-vapor adsorption.

Effect of kind and source of dye on adsorption.— In searching for a dye that would be adsorbed by colloidal ferric oxide, dyes from twenty-three sources were examined. The tests were made in both distilled water and approximately 0.1-per-cent ammonia water. Some of the dyes used are tabulated by various writers as acid dyes, and theoretically, therefore, would be adsorbed strongly by colloidal ferric oxide, which is basic. Only one, however, of all those examined was found to be adsorbed sufficiently strongly by colloidal ferric oxide to warrant its use. This was diamine sky-blue.

The effect of the small amount of ammonia on adsorption was very noticeable in some instances. In some cases it increased adsorption; in other cases it decreased adsorption; and in still others it changed the intensity or color of the dye. The effect of electrolytes on the adsorption of dyes was pointed out by Bancroft (1914), and should not be ignored in working with soils.

Effect of the chemical composition of minerals on dye adsorption.— During the experimentation on the adsorption of dyes by artificially prepared colloids, it was found that the chemical composition of the material had a great deal to do with the adsorption. For instance, methylene blue, a basic dye, is adsorbed strongly by colloidal silica but not at all by colloidal ferric oxide; whereas diamine sky-blue, an acid dye, acts in just the opposite way with respect to these two materials. In other words, according to this fact, neither dye is sufficient for measuring the total colloidal content of the soil, provided that approximately pure colloidal silica and ferric oxide are present.

In this connection it was thought advisable to ascertain whether the chemical composition of certain soil-forming minerals is an important factor in their adsorption of dyes. The minerals listed in table 3 were finely ground, and 1-gram samples were shaken with equal quantities of dyes. As far as it was possible to make them, the checks of the two dyes were of the same intensity.

TABLE 3. ADSORPTION OF METHYLENE BLUE (BASIC DYE) AND DIAMINE SKY-BLUE (ACID DYE) BY SOIL-FORMING MINERALS
(Relative intensities of solutions after adsorption shown)

Mineral	Methylene blue	Diamine sky-blue
Ground quartz SiO_2	23.0±0.8	22.5±0.4
Halloysite $H_4Al_2Si_2O_9 \cdot H_2O$	355.0±4.0	40.0±0.0
Pyrophyllite $H_2Al_2(SiO_3)_4$	46.0±0.0	23.0±0.8
Kaolinite $2SiO_2 \cdot Al_2O_3 \cdot 2H_2O$	Clear	120.0±4.3
Prehnite $H_2Ca_2Al_2(SiO_4)_3$	27.5±0.4	26.5±0.4
Natrolite $Na_2Al_2Si_3O_{10} \cdot 2H_2O$	26.5±0.4	25.0±0.0
Siderite $FeCO_3$	24.0±0.8	34.0±0.0
Hematite Fe_2O_3	34.0±0.0	29.0±0.8
Limonite $2Fe_2O_3 \cdot 3H_2O$	23.0±0.8	75.0±0.0
Calcium sulfate $CaSO_4$	22.0±0.0	38.0±0.8
Calcium carbonate $CaCO_3$	22.0±1.7	45.0±0.8
Calcium hydrate $Ca(OH)_2$	*16.0±1.7	Clear
Check	25.0	25.0

* Purplish tinge. Difficult to read.

It can be seen that, in general, the adsorption of methylene blue is greater by the acid minerals. Kaolinite shows the greatest adsorption of this dye, and acts more like colloidal silica than does ground quartz, which adsorbs very little.

With diamine sky-blue the correlation between chemical composition and dye adsorption is less well marked. However, calcium hydrate, the most basic, is also the most adsorptive of this dye. In this case flocculation probably plays a part. Kaolinite adsorbs this dye more strongly than would be suspected from its composition. It is very likely that the great amount of internal surface of this mineral overrides any chemical effect on adsorption.

Rohland (1914) has pointed out that certain classes of dyes are adsorbed by certain kinds of soils.

Effect of lower forms of plant life on dye adsorption.— In the course of the experiment some results were obtained indicating that the plant life which had grown in the soil was affecting the adsorption of dyes. It was known that certain dyes are used by plant physiologists and bacteriologists in staining organisms. In order to get definite data on this point an experiment was run, using a fungus and an alga. That the possible effect of the soluble matter on the dye might be done away with,

a water extract of the material was used as a check. Results are given in table 4:

TABLE 4. ADSORPTION OF DYES BY LOWER FORMS OF PLANT LIFE

Dye used	$(C-C_1)\cdot$dye adsorbed by water extract	$(C-C_1)\cdot$dye adsorbed by water extract plus fungus or alga	Difference
(a) A fungus (Botrytis)			
Methylene blue	78.7±0.2	91.9±0.16	13.2±0.26
Diamine sky-blue	83.6±0.5	92.6±0.22	9.0±0.55
Malachite green	80.0±0.0	95.8±0.06	15.8±0.06
(b) An alga (Cladophora)			
Methylene blue	797.9±3.3	993.8±0.03	195.9±3.3
Diamine sky-blue	824.5±2.5	960.0±....*	135.5±...*
Malachite green	877.2±2.0	933.3±1.87	56.1±2.7

* No probable error. Cloudy. Difficult to read.

The differences are significant, and from them it is evident that both alga and fungus adsorb dye. The alga was found to be very adsorptive. Therefore, in dye-adsorption experiments where there is a chance for these organisms to grow, they should be taken into consideration.

The point just made is further substantiated by the data presented in table 5. The treatment of the soils was the same except for sterilization. They were allowed to remain moist for several months after sterilization and before the dye-adsorption experiment.

TABLE 5. EFFECT OF PREVIOUS STERILIZATION ON THE ADSORPTION OF METHYLENE BLUE BY DUNKIRK SURFACE SOIL

	$(C-C_1)\cdot$dye adsorbed	Difference
Sterilized, no growth apparent	82.25±0.38	6.75±0.39
Not sterilized, growth apparent	89.00±0.03	

Methods used in this work

At the outset the writer was of the opinion that some of the colloidal states could best be measured by certain methods and other states by

other methods. For example, a colloid in the dry state can perhaps best be measured by an adsorption of water vapor, since the adsorption of a dye from solution would introduce the possible effect of free water on the condition. In the moist condition, on the other hand, the dye-adsorption method would not have that disadvantage at least. It was also thought wise to attack the problem with as many methods as were reasonably practicable. Results obtained during the course of the experimentation strengthened these opinions.

Three methods were used: (1) a slight modification of Mitscherlich's water-vapor-adsorption method; (2) a modification of Ashley's dye-adsorption method; and (3) the suspension method. The first and the second method were used the most extensively. The details of each method as finally worked out and used are as follows:

The water-vapor-adsorption method.— Five-gram portions of oven-dried soil or the equivalent were spread out as uniformly as possible in petri dishes having a diameter of approximately 10 centimeters. This gave in each dish a layer of soil with an average thickness of less than 1 millimeter.

The dishes with the soil were placed in desiccators containing a little 10-per-cent sulfuric acid in the lower part. By setting the dishes one on another, from five to seven dishes could easily be placed in the small desiccators and twice that number in the large desiccators. Mitscherlich used only one dish to a desiccator, which made the method exceedingly slow.

The dishes were separated from one another by mats of cotton cloth which had been saturated with the acid solution, the excess being removed by wringing. Each mat was kept from touching the soil in the dish below by means of a support made from a piece of cardboard and dipped into hot paraffin. The mats served to hasten the vaporization in the immediate vicinity of the soil. On the inner sides of the desiccators (humidifiers, properly speaking) were broad strips of cotton cloth, which were held in place by air pressure and adhesion and which dipped into the acid solution beneath. These served to bring up the liquid and hasten vaporization.

Hilgard (1911) used a wooden box, the sides of which were lined with blotting paper moistened with water to insure saturation of the air. Mitscherlich (1905) used 10-per-cent sulfuric acid in the bottom of the desiccator, but no strips of cloth or paper to hasten vaporization.

The soils were exposed to the vapor of the acid solution for one week (Mitscherlich found five days sufficient), at room temperature in the desiccator, which had previously been evacuated with a suction pump until the vapor pressure was approximately 2 centimeters of mercury. After exposure of the soils for one week, air was allowed to enter the desiccator very slowly. If air is allowed to enter rapidly, the cooling effect due to its rapid expansion causes a condensation of water vapor on the contents of the desiccator.

The soils were then quickly poured and brushed into previously weighed bottles fitted with ground glass stoppers. It was computed that the time during which the soil was exposed to the drying influence of the air was less than ten seconds. In that time the loss of water by evaporation is negligible.

The soil was dried at a temperature of 105° C. and weighed, and the loss of water was computed as a percentage of the oven-dry weight. This is hygroscopic water, and the amount present has been considered by Mitscherlich and others to depend upon the extent of surface of the soil. It has therefore been considered a measure of the colloidal content, and is so considered in this work.

Owing to the high experimental error, which was experienced even with the exercise of the greatest care, it was decided to run several replicates of each test. Usually five replicates of each treatment were run. In order to make experimental conditions as uniform as possible for the different treatments, at least one test of each treatment was put in the same desiccator, and in the different desiccators the relative positions of these tests were changed.

The dye-adsorption method.— Five-gram portions of oven-dry soil or its equivalent were used with the dye-adsorption method. The amount of dye used varied with both the kind of dye and the soil. It was necessary to run a preliminary test for each dye and soil in order to ascertain how much of the dye or its concentration was necessary.

The dye solution and the soil were put into a shaker bottle such as is used in the mechanical analysis of soils (Lyon, Fippin, and Buckman, 1915), and the volume was brought up to 150 mils by means of distilled water. This was shaken in a mechanical shaker for thirty minutes, it

having been ascertained that this amount of shaking gave a maximum, or very nearly maximum, adsorption.

After removal from the shaker, the bottle and its contents were allowed to stand for a few minutes, until the bulk of the soil had settled. A portion of the supernatant suspension, about 50 mils, was poured into a centrifuge tube (together with a few mils of 1-per-cent alum solution when methylene blue was used as the dye), and was centrifuged until clear. With diamine sky-blue a flocculant could not be used because of its effect on the dye.

After clarification the supernatant dye solution was compared with a standard dye solution in a colorimeter, and from these readings and the strengths of dye used the amount of dye adsorbed was computed.

This method differs from Ashley's original method particularly in regard to the kind of dye used and the addition of a flocculant to clarify the suspension. It was found impossible to clarify some suspensions without a flocculant, even by centrifuging at high speed for several hours or by letting the suspension stand for several days.

The suspension method.— Suspensions were made by shaking the soil in the medium used for thirty minutes, allowing it to stand for thirty minutes, evaporating an aliquot portion of the suspension, drying, and weighing. Both distilled water and 4-per-cent ammonium hydroxide were used as the dispersion media.

Experiments with artificially prepared colloids

Colloidal silica, alumina, and ferric oxide were prepared by the ordinary precipitation methods and were washed free of electrolytes with distilled water. Humus was prepared from muck by extracting the bases with hydrochloric acid, washing out the excess acid, and deflocculating with ammonia. The greater part of the excess ammonia was washed out with the water.

The object of the experiment was to ascertain the effect of drying upon the adsorption of dyes by the colloidal materials most commonly found in soils.

Each of the materials was divided into three equal lots. Each lot was subjected to different treatment and was divided into four replicates.

The treatments consisted of keeping moist, air-drying, and oven-drying (105° C.). The results of the experiment are given in table 6:

TABLE 6. ADSORPTION OF DYES BY ARTIFICIALLY PREPARED SOIL COLLOIDS

	Time in contact	Moist		Air-dried		Oven-dried	
		(C–C₁) · dye	Difference	(C–C₁) · dye	Difference	(C–C₁) · dye	Difference
Silica and methylene blue	1 day	81.3±2.4	7.6±2.5	88.4±0.1	11.6±0.1	88.5±0.8	5.9±0.9
	8 days	73.7±0.5	14.5±0.9	100.0 ...	Trace	94.4±0.3	5.6±0.3
	15 days	59.2±0.7		100.0 ...		100.0 ...	
Humus and methylene blue	1 day	89.8±0.1	0.2±0.1	85.8±0.4	1.2±0.5	86.3±0.0	0.4±0.2
	8 days	90.0±0.0	0.6±0.0	84.6±0.2	2.6±0.6	85.9±0.2	3.2±0.3
	15 days	90.6±0.0		87.2±0.6		89.1±0.2	
Ferric oxide and diamine sky-blue	1 day	100.0 ...	0.0 ...	82.0±0.1	2.2±0.5	83.2±0.4	4.5±0.7
	8 days	100.0 ...	0.0 ...	84.2±0.5	0.9±0.7	87.7±0.6	2.8±0.8
	15 days	100.0 ...		85.1±0.6		90.5±0.6	
Alumina and diamine sky-blue	1 day	100.0 ...	0.0 ...	79.9±0.1	2.9±0.8	80.4±0.3	2.9±0.3
	8 days	100.0 ...	0.0 ...	82.8±0.7	0.7±0.8	83.3±0.0	0.7±0.5
	15 days	100.0 ...		83.5±0.4		84.0±0.5	

It is seen that in the moist material, with the possible exception of humus, maximum adsorption was reached in one day, and with silica there was a reversal of the adsorption process as the time elapsed. In both the air-dried and the oven-dried materials, with two exceptions, the amount of adsorption increased with the lapse of time. In most cases the differences are significant. They show that the condition of these colloids caused by drying is reversed by their standing in water, and that the reversal requires time.

Van Bemmelen (1909) has shown that the dried oxides of various metals will take up water vapor, and that there is a reversibility in this respect along some lines. The data in table 7 show the same thing for the commonest soil colloids, and also give a comparison of their relative adsorption of water vapor in three days:

TABLE 7. ADSORPTION OF WATER VAPOR BY AIR-DRIED, ARTIFICIALLY PREPARED, SOIL COLLOIDS

Per cent of water vapor adsorbed by			
Ferric oxide	Alumina	Humus	Silica
9.5 ± 0.4	10.25 ± 0.6	30.7 ± 0.0	58.1 ± 0.25

Principal soils used

Two surface soils and two subsoils were used in these experiments. These soils, consisting of Dunkirk surface soil, Clyde surface soil, Dunkirk subsoil, and Vergennes subsoil, represent a range of conditions. Their mechanical analyses, according to the centrifugal method of the United States Bureau of Soils, are given in table 8:

TABLE 8. MECHANICAL ANALYSES OF PRINCIPAL SOILS USED IN EXPERIMENTAL WORK

	Dunkirk surface soil (per cent)	Clyde surface soil (per cent)	Dunkirk subsoil (per cent)	Vergennes subsoil (per cent)
Fine gravel	0.170	0.145	0.000	0.020
Coarse sand	0.305	1.055	0.260	0.045
Medium sand	0.690	3.925	0.605	0.080
Fine sand	2.270	9.895	1.145	0.735
Very fine sand	9.590	11.525	12.145	1.595
Silt	74.030	53.330	65.800	22.960
Clay	12.945	20.125	20.045	74.565

The Dunkirk surface soil was obtained from Caldwell Field, Cornell University. According to the textural classification (Lyon, Fippin, and Buckman, 1915) of the United States Bureau of Soils, it is a silt loam. The sod was removed and the soil was taken from three to twelve inches below the surface.

The Clyde surface soil came from another field on the university farm, and represents a phase of the Dunkirk series which is rich in organic matter. These soils are naturally poorly drained and are much darker in color than the soils of the Dunkirk series proper. In getting the sample the sod was removed, as in the case of the Dunkirk surface soil. Texturally the Clyde soil is a silty clay loam.

The Dunkirk subsoil was taken at a depth of from one to two feet directly beneath the surface soil of the same series mentioned above. It is a silty clay loam texturally.

The Vergennes subsoil was obtained from Washington County, New York. Like the soils described above, it is a glacial lake soil, and, up to 1911 at least, it was the heaviest soil mapped by the United States Bureau of Soils. The sample was taken at a depth of from one to two feet. Texturally the soil is a clay.

The organic matter and the humus content of these soils are given in table 9. These were determined according to the official methods described in Bulletin 107 of the United States Bureau of Chemistry, with the exception that ammonium carbonate was used to flocculate the clay in the ammonia extract of humus as suggested by Rather (1911).

TABLE 9. ORGANIC MATTER (LOSS BY IGNITION) AND HUMUS OF PRINCIPAL SOILS USED IN EXPERIMENTAL WORK

Soil	Organic matter (per cent)	Humus (per cent)
Dunkirk surface	5.085	1.265
Clyde surface	14.540	4.340
Dunkirk subsoil	3.055	0.205
Vergennes subsoil	5.795	0.495

Preparation of samples.— After the soils were brought to the laboratory they were dried to a condition in which they could be worked readily without sticking, and then put thru a 2-millimeter sieve. Each lot of soil was then thoroly mixed before samples were selected for individual treatments. Certain lots were kept moist thruout the experimentation by placing them in air-tight jars; other lots were subjected to air-drying at room temperature and at 105° C.— the former being designated as *air-dried* and the latter as *oven-dried.*

The air-dried samples were usually dried by spreading the soil out in enameled pans in layers about $\frac{1}{4}$ inch deep. A layer of soil as thin as this usually dries very quickly. In case of alternate wetting and drying, the wetting was done with distilled water. No attempt was made to bring the soils to a definite moisture content; this was thought not worth

while, as such action does not occur in nature. The soils were saturated or a slight excess of water was added. The dried soils were usually lumpy, and before sampling they were crushed by means of a wooden rolling-pin.

Effect of various factors on hygroscopicity

It has been shown by Ehrenberg and Pick (1911) that dried soils adsorb less moisture than do moist soils, and these authors used this fact as an argument against Mitscherlich's method of determination of hygroscopic moisture. It is not known whether the difference is due to the effect of drying upon the colloidal material, or to the layer of adsorbed air on the soil (Ehrenberg, 1915).

Effect of time.— In order to learn whether this difference in hygroscopicity persists thruout a period of three months at least, an experiment was run to cover that point. The data are given in table 10:

TABLE 10. EFFECT OF TIME ON THE ADSORPTION OF WATER VAPOR BY CLYDE SURFACE SOIL

Length of time in humidifier	Soil treatment	Per cent of water adsorbed	Difference	Ratio
1 month	Air-dried	12.15±0.30	3.80±0.48	1.31±0.045
	Moist	15.95±0.38		
2 months	Air-dried	12.20±0.25	4.80±0.49	1.39±0.04
	Moist	17.00±0.42		
3 months	Air-dried	12.70±0.10	4.05±0.32	1.32±0.03
	Moist	16.75±0.30		

It is seen that the differences do persist as long as three months and that they are significant. Also, the ratios between the hygroscopicities at different periods are about constant. If the difference in hygroscopicity between moist and dry soil as shown by a test of one month is due to a failure to establish equilibrium, it seems that this failure still persists at the end of three months.

Effect of remoistening.— The second question to be studied was whether this drying produces a permanent effect on the hygroscopicity of the soil. Does remoistening restore the original condition? The data on this point are given in table 11. In order to preclude the possible effect of a failure to establish equilibrium, the remoistened soils were brought to a higher

moisture content than that of the continuously moist and undried soils with which they were compared. The comparison between any two conditions of the same soil were made in the humidifier at the same time.

TABLE 11. Effect of Remoistening Soils on their Adsorption of Water Vapor

Soil	Original water content (per cent)	Treatment	Per cent of water adsorbed	Difference
Dunkirk surface	10.7	Continuously moist	3.80±0.03	0.42±0.08
	25.0	Air-dried and remoistened	3.38±0.05	
Clyde surface	42.0	Continuously moist	18.9 ±0.2	3.1 ±0.04
	48.7	Air-dried and remoistened	15.8 ±0.3	
Dunkirk subsoil	17.8	Continuously moist	5.77±0.01	0.51±0.02
	18.7	Air-dried and remoistened	5.26±0.02	
Vergennes subsoil	18.9	Continuously moist	17.60±0.05	0.20±0.07
	25.3	Air-dried and remoistened	17.40±0.05	

In every case the remoistened soils contained less hygroscopic moisture at the end of a week than did the continuously moist soils, altho the remoistened soils held more water at the beginning of the experiment. The differences, according to the standard set (footnote, page 492), are significant in all cases except that of the Vergennes soil, in which case the chances are 10 to 1 in favor of the continuously moist soil (Wood and Stratton, 1910).

These data indicate rather clearly that in the case of the air-dried soils the hygroscopicity is not immediately restored by remoistening. It may be observed that the greatest difference here is with the soil containing the greatest amount of organic matter and humus — the Clyde surface soil (table 9, page 502).

Altho it cannot be definitely stated whether these differences in water-vapor adsorption are due to the effect of drying on the colloidal matter or to the effect of drying on the adsorbed air, if it be assumed that the effect is on the total surface of the soil there is strong evidence of its being more or less permanently diminished by air-drying. In other words, the change due to drying out is not an immediately reversible one.

Permanency of the effect of drying.— It was next attempted to ascertain the permanency of this effect of air-drying. Some of the same soils used

in the preceding experiment were kept in air-tight bottles for three months and were then subjected to determinations of hygroscopicity. The results are given in table 12:

TABLE 12. ADSORPTION OF WATER VAPOR BY CONTINUOUSLY MOIST AND BY REMOISTENED SOILS, THREE MONTHS AFTER REMOISTENING

Soil	Treatment	Per cent of water adsorbed	Difference
Dunkirk surface	Continuously moist	4.29±0.02	0.39±0.02
	Remoistened	3.90±0.01	
Clyde surface	Continuously moist	18.80±0.01	2.10±0.01
	Remoistened	16.70±0.01	

These data show that after three months the hygroscopicity of the remoistened soils did not return to a value equal to that of the continuously moist soils, indicating that with these soils the effect of drying on this property is not reversible within three months at least.

Effect of alternate wetting and drying.—The next experiment was in regard to the effect of alternate wetting and drying. The data are given in table 13:

TABLE 13. EFFECT OF ALTERNATE WETTING AND DRYING OF SOILS UPON THEIR ADSORPTION OF WATER VAPOR

Soil	Treatment	Per cent of water vapor adsorbed	Difference
Dunkirk surface	Continuously moist	3.97±0.07	
			0.99±0.08
	Air-dried 1 time	2.98±0.04	
			0.05±0.06
	2	2.93±0.04	
			0.07±0.04
	4	2.86±0.02	
			0.08±0.09
	8	2.78±0.09	
			0.06±0.10
	16	2.84±0.05	
			0.10±0.06
	32	2.94±0.04	
	Difference between 1 drying and 32 dryings	....	0.04±0.06

TABLE 13 (*concluded*)

Soil	Treatment	Per cent of water vapor adsorbed	Difference
Clyde surface	Continuously moist	17.20±0.4	
	Air-dried 1 time	11.10±0.2	6.10±0.4
	2	11.10±0.4	0.00±0.4
	4	10.50±0.3	0.60±0.5
	8	10.80±0.3	0.30±0.4
	16	10.70±0.2	0.10±0.4
	32	10.70±0.3	0.00±0.4
	Difference between 1 drying and 32 dryings	....	0.40±0.4
Dunkirk subsoil	Continuously moist	5.97±0.07	
	Air-dried 1 time	4.11±0.06	1.86±0.09
	2	4.10±0.03	0.01±0.07
	4	4.02±0.04	0.08±0.05
	8	3.95±0.02	0.07±0.04
	16	3.86±0.02	0.09±0.03
	32	3.80±0.05	0.06±0.05
	Difference between 1 drying and 32 dryings	....	0.31±0.08
Vergennes subsoil	Continuously moist	17.90±0.03	
	Air-dried 1 time	13.30±0.02	4.60±0.04
	2	13.00±0.10	0.30±0.10
	4	12.50±0.13	0.50±0.16
	8	12.50±0.08	0.00±0.14
	16	11.90±0.08	0.60±0.11
	32	11.90±0.04	0.00±0.09
	Difference between 1 drying and 32 dryings	....	1.40±0.04

With all the soils the differences between the percentages of water vapor adsorbed by moist and by air-dried soils are sufficiently great to be significant; but, except in one case — between eight and sixteen dryings of the Vergennes subsoil — the differences between successive dryings are not significant.

Comparing the cumulative effect of thirty-two dryings with the effect of one drying, it is to be seen that the difference is significant with the two subsoils but not with the surface soils. Perhaps the surface soils do not show the cumulative effect because, owing to their natural subjection to the alternate wetting and drying actions, a sort of equilibrium has been established.

No crushing tests were run on these soils, but it was observed while crushing them with the rolling-pin that in general the soils which had been dried the greatest number of times crushed the most easily. This observation agrees with Fippin's (1911) penetration tests on alternately wetted and dried soils.

It was observed also that a mold made its appearance on the Dunkirk and Clyde soils, the two containing the most humus, after about eight wettings and dryings. This is probably due to an increased solubility of the organic matter caused by the treatments.[2]

Effect of drying at high temperatures.— Data on the effect of drying at high temperatures are given in table 14:

TABLE 14. ADSORPTION OF WATER VAPOR BY SOILS DRIED AT HIGH TEMPERATURES

Soil	Treatment	Per cent of water vapor adsorbed	Difference
Dunkirk surface	Air-dried	3.02±0.01	
			0.41±0.02
	Oven-dried	2.61±0.02	
			1.50±0.02
	Ignited	1.11±0.01	
Clyde surface	Air-dried	11.60±0.05	
			1.10±0.05
	Oven-dried	10.50±0.02	
			5.28±0.04
	Ignited	5.22±0.03	

[2] It is shown later (page 516) that the drying of the soils increases the solubility of their organic matter.

TABLE 14 (*concluded*)

Soil	Treatment	Per cent of water vapor adsorbed	Difference
Dunkirk subsoil	Air-dried	3.98±0.03	0.27±0.04
	Oven-dried	3.71±0.03	0.93±0.04
	Ignited	2.78±0.03	
Vergennes subsoil	Air-dried	13.20±0.08	0.40±0.09
	Oven-dried	12.80±0.08	3.69±0.04
	Ignited	9.11±0.02	

The following points are shown by the above data: (1) Igniting soils does not destroy their ability to take up moisture from a more or less saturated atmosphere, contrary to frequent assertions that it does. In fact, some of the ignited soils have rather high hygroscopicity. (2) The differences between air-dried and oven-dried conditions are smaller than those between oven-dried and ignited conditions. (3) The hygroscopic values of the soils richest in humus, the surface soils, have suffered the most by ignition.

Effect of long immersion in water.— Soils that were continuously air-dried were compared with the same kinds of soils that had been air-dried and then covered with an excess (200 per cent) of water for two years. The soils that had stood under water were again air-dried before being compared with those that were continuously air-dried. The results are given in table 15.

The differences, which are significant in each case, are not in the same direction. The long soaking has increased the adsorptive capacity of the Dunkirk soil, perhaps by a hydrolysis of the inorganic constituents, producing the colloidal condition.

The decrease in the adsorptive capacity of the Clyde soil can be accounted for by the decomposition of the colloidal organic matter, which was contained in this soil to a greater extent than in the Dunkirk soil. This decrease in colloidal content may override any increase thru

hydrolysis. It was observed that bacterial activity, as judged by the appearance of gases, was especially great in the Clyde soil. That previous drying of a soil increases its bacterial activity has been shown by Klein (1915) and by others.

TABLE 15. ADSORPTION OF WATER VAPOR BY SOILS IMMERSED IN WATER FOR TWO YEARS

Soil	Treatment	Per cent of water vapor adsorbed	Difference
Dunkirk surface	Air-dried	2.77±0.02	0.13±0.02
	Under water	2.90±0.01	
Clyde surface	Air-dried	10.50±0.003	0.40±0.005
	Under water	10.10±0.004	

Effect of leaching.— The effect of leaching on the colloidal content of soils is of more importance than the amount of work done on this point would indicate. It was studied only briefly. The data are presented in table 16:

TABLE 16. ADSORPTION OF WATER VAPOR BY LEACHED AND BY UNLEACHED SOIL

Soil treatment	Per cent of water vapor adsorbed	Difference
Leached	4.46±0.01	1.44±0.02
Unleached	3.02±0.02	

Dye-adsorption experiments

The dye-adsorption experiments were carried on with the same kinds of soils and some of the same treatments as have already been mentioned in connection with water-vapor-adsorption experiments.

Data showing the effect of alternate wetting and drying of soils on their adsorption of methylene blue are presented in table 17:

TABLE 17. EFFECT OF ALTERNATE WETTING AND DRYING OF SOILS ON THEIR ADSORPTION OF METHYLENE BLUE

Soil	Treatment	Corrected colorimetric reading	Milligrams of dye adsorbed per gram of soil	Difference
Dunkirk surface	Continuously moist....	53.5±1.7	4.870±0.004	
	Air-dried 1 time......	135.0±1.4	4.950±0.0005	0.080±0.004
	2	125.0±2.4	4.945±0.001	0.005±0.001
	4	133.0±2.4	4.950±0.001	0.005±0.001
	8	133.0±4.1	4.950±0.002	0.000±0.002
	16	138.0±2.0	4.950±0.0005	0.000±0.002
	32	131.0±2.4	4.950±0.001	0.000±0.001
	Oven-dried once.......	88.0±0.0	4.920±0.000	0.030±0.001
	Ignited...............	6.8±0.1	3.985±0.015	0.935±0.015
	Difference between 1 drying and 32 dryings	....	....	0.000±0.001
Clyde surface	Continuously moist....	50.5±0.2	9.97±0.000	
	Air-dried 1 time......	115.8±0.6	9.99±0.000	*0.02±0.000
	2	133.0±0.6	9.99±0.000	0.00±0.000
	4	155.8±2.6	9.99±0.000	0.00±0.000
	8	146.0±2.0	9.99±0.000	0.00±0.000
	16	140.2±4.8	9.99±0.000	0.00±0.000
	32	151.5±2.2	9.99±0.000	0.00±0.000
	Oven-dried once.......	92.8±0.6	9.98±0.000	0.01±0.000
	Ignited...............	3.1±0.0	9.53±0.030	0.45±0.030
	Difference between 1 drying and 32 dryings	....	....	0.00±0.000

* In cases when the probable error of the mean is 0.000, separate determinations were so close as to make it negligible.

TABLE 17 (*concluded*)

Soil	Treatment	Corrected colorimetric reading	Milligrams of dye adsorbed per gram of soil	Difference
Dunkirk subsoil	Continuously moist....	52.9 ±0.8	9.91±0.002	
				0.09±0.003
	Air-dried 1 time......	26.0 ±0.0	9.82±0.002	
				0.02±0.003
	2	28.9 ±0.1	9.84±0.002	
				0.00±0.004
	4	28.6 ±0.3	9.84±0.003	
				0.00±0.004
	8	28.3 ±0.4	9.84±0.003	
				0.00±0.004
	16	29.4 ±0.3	9.84±0.003	
				0.00±0.009
	32	28.25±0.7	9.84±0.009	
				0.11±0.010
	Oven-dried once.......	17.0 ±0.2	9.73±0.005	
				2.88±0.041
	Ignited...............	1.5 ±0.0	6.85±0.041	
	Difference between 1 drying and 32 dryings	....	....	0.02±0.009
Vergennes subsoil	Continuously moist....	54.9 ±1.9	39.90±0.004	
				0.00±0.004
	Air-dried 1 time......	54.75±0.7	39.90±0.000	
				0.00±0.000
	2	54.75±0.7	39.90±0.000	
				0.00±0.000
	4	61.4 ±0.5	39.90±0.000	
				0.02±0.000
	8	50.4 ±0.8	39.88±0.000	
				0.05±0.000
	16	81.5 ±1.6	39.93±0.000	
				0.05±0.000
	32	93.4 ±2.6	39.98±0.000	
				0.22±0.000
	Oven-dried once.......	24.0 ±0.3	39.76±0.000	
				31.88±0.000
	Ignited...............	0.2 ±0.0	7.88±0.000	
	Difference between 1 drying and 32 dryings	....	....	0.08±0.000

These results are rather irregular, and, on the whole, inconsistent. With the two surface soils there is an increase in their adsorptive capacities due to one air-drying, a result just opposite to that obtained by the water-vapor-

adsorption method. The Dunkirk subsoil shows a decrease in adsorptive capacity due to one air-drying, and the Vergennes soil shows no effect.

The differences between successive dryings are in many cases significant, but the results are so erratic as to justify no conclusions. With the two surface soils the cumulative effect of thirty-two dryings is nil, but with the two subsoils the cumulative effect is great enough to be significant in one case. This last observation is not in accord with the one on the same point under hygroscopicity.

The effects of oven-drying and ignition are very marked in all cases, there being a decrease in adsorption in going from the air-dry to the oven-dry and to the ignited conditions. The differences are more marked with the subsoils than with the surface soils.

A point which stands out in comparing the results obtained by this method with those obtained from the water-vapor-adsorption method is that the Clyde soil shows the least changes in its adsorptive capacity due to drying. Even the ignited Clyde soil adsorbs nearly as much as the same soil under other conditions.

As already stated, a glacial clay subsoil was thrown out of the hygroscopicity experiments because of its unusual adsorptive capacity. This soil was subjected to dye-adsorption tests. The results are given in table 18:

TABLE 18. Adsorption of Methylene Blue by a Glacial Clay Subsoil Variously Treated

Soil treatment	Corrected colorimetric reading	Milligrams of dye adsorbed per gram of soil	Difference
Continuously moist	50.0 ±0.1	19.88±0.002	
			0.05±0.002
Air-dried 1 time	35.6 ±0.5	19.83±0.002	
			0.03±0.002
8	30.25±0.3	19.80±0.002	
			0.01±0.002
16	30.9 ±0.3	19.81±0.002	
			0.02±0.004
32	28.5 ±0.6	19.79±0.004	
			0.00±0.004
Oven-dried once	20.25±0.1	19.79±0.002	
Difference between 1 drying and 32 dryings			0.04±0.004

The differences between successive drying treatments are significant in every case except between air-drying and oven-drying, but the changes due to successive air-drying are not always in the same direction. The cumulative difference due to thirty-two dryings as compared with one drying is significant. The results are not wholly in accord with those of other soils similarly treated.

In table 19 are given the effects of long immersion of soils on their adsorptive capacity for methylene blue:

TABLE 19. ADSORPTION OF METHYLENE BLUE BY SOILS IMMERSED IN WATER FOR TWO YEARS

Soil	Treatment	Corrected colorimetric reading	$(C-C_1) \cdot$ dye adsorbed per gram of soil	Difference
Dunkirk surface	Air-dried	25.0±0.1	60.0±0.16	14.4±0.21
	Under water	39.1±0.2	74.4±0.13	
Clyde surface	Air-dried	51.9±0.6	80.7±0.22	8.6±0.22
	Under water	93.5±0.4	89.3±0.04	

The long soaking under water has increased the adsorptive capacities of these soils. The results with the Dunkirk soil agree with those obtained by water-vapor adsorption, while those with the Clyde soil do not.

Adsorption of methylene blue by leached and by unleached soil is shown by table 20:

TABLE 20. ADSORPTION OF METHYLENE BLUE BY LEACHED AND BY UNLEACHED SOIL

Soil treatment	Corrected colorimetric reading	$(C-C_1) \cdot$ dye adsorbed per gram of soil	Difference
Leached	189.0±3.0	94.7±0.84	8.2±0.84
Unleached	74.1±0.3	86.5±0.06	

Leaching has increased the adsorptive capacity of this soil for this dye. The results agree with those obtained by the water-vapor-adsorption method.

Owing to the opposite behavior of the diamine sky-blue with the different artificially prepared colloidal materials as compared with methylene blue, it was decided to ascertain the effect of moisture changes on the capacity of the soils for this dye. The results are given in table 21:

TABLE 21. EFFECT OF DRYING SOILS ON THEIR ADSORPTION OF DIAMINE SKY-BLUE

Soil	Treatment	Corrected colorimetric reading	Milligrams of dye adsorbed per gram of soil	Difference
Dunkirk surface	Continuously moist	52.00±0.7	0.42±0.008	
				0.05±0.011
	Air-dried once	47.40±0.5	0.37±0.007	
				0.24±0.008
	Oven-dried once	75.40±0.6	0.61±0.003	
				0.03±0.009
	Ignited	71.50±1.4	0.58±0.008	
Clyde surface	Continuously moist	49.75±0.4	0.78±0.026	
				0.43±0.032
	Air-dried once	73.10±0.8	1.21±0.018	
				0.02±0.027
	Oven-dried once	71.75±1.0	1.19±0.020	
				0.46±0.039
	Ignited	45.60±0.8	0.73±0.034	
Dunkirk subsoil	Continuously moist	49.25±2.0	4.16±0.035	
				0.10±0.036
	Air-dried once	56.10±0.6	4.26±0.010	
				0.05±0.018
	Oven-dried once	60.25±1.2	4.31±0.015	
				0.29±0.035
	Ignited	42.50±1.2	4.02±0.030	
Vergennes subsoil	Continuously moist	48.25±0.9	3.81±0.035	
				0.43±0.042
	Air-dried once	76.00±1.6	4.24±0.025	
				0.06±0.032
	Oven-dried once	70.40±0.7	4.18±0.020	
				4.01±0.163
	Ignited	11.95±0.3	0.17±0.150	

The effect of air-drying once was to decrease the adsorption by the Dunkirk surface soil and to increase it with the other soils. As between

the air-dry and the oven-dry condition, there is an increase with one surface soil and one subsoil, and a decrease with the other two; the differences are significant, however, with one soil only, the Dunkirk surface soil. Between the oven-dried and the ignited condition there is a decrease which is significant in every case but one. The only point which stands out clearly is that ignition decreases the adsorption of this dye. By comparing the results with those given in table 17 (page 510–511), it is seen that all these soils adsorb less of this dye than of methylene blue.

Suspension experiments

The suspension method is described on page 499. The results of the experiments with this method are given in table 22:

TABLE 22. Per Cent of Clyde Soil Remaining in Suspension in Distilled Water Thirty Minutes after Shaking

Soil treatment	In distilled water	In 4-per-cent ammonia
Continuously moist	9.15	21.90
Air-dried 1 time	6.55	17.10
16	3.40	7.35
32	3.70	7.75
Oven-dried once	4.80	9.45

In both distilled water and ammonia the moist soil was deflocculated the most, and the soil that was air-dried once was deflocculated more than those that were air-dried sixteen or thirty-two times. The deflocculating influence of the ammonia was very marked. These results show that the flocculated condition is not immediately reversible, even with shaking in water.

Additional experiments

Owing to the striking influence of drying on the colloidal matter of the Clyde soil, as shown by the experiments in water-vapor adsorption and as mentioned in the literature, it was thought probable that differences in the amount of humus extractable by ammonia could be found. With

this in mind an experiment was planned. The method used is described on page 502. The results are given in table 23:

TABLE 23. EFFECT OF ALTERNATE WETTING AND DRYING UPON THE AMOUNT OF HUMUS EXTRACTED FROM A CLYDE SOIL

Soil treatment	Per cent of humus extracted
Continuously moist	4.40
Air-dried 1 time	4.42
2	4.44
4	4.34
8	4.48
16	4.18

The differences are not great enough to warrant drawing a conclusion that the moisture changes affected the amount of humus extracted by this method. It is very likely that the treatment, as the purpose for which it was designed would lead one to believe, took out all the humus. The extraction by this method is probably so thoro as to mask any small differences that might exist as a result of moisture changes.

The data given in table 24 were obtained by comparing, colorimetrically, distilled water extracts, which were filtered thru a porcelain filter. The results show that air-drying these soils has increased the solubility of the coloring matter of the humus, if not the humus itself.

TABLE 24. RELATIVE INTENSITIES OF WATER EXTRACTS OF DUNKIRK AND CLYDE SURFACE SOILS

Soil	Moist	Air-dried	Difference
Dunkirk surface	50	20.8±2.5	29.2±2.5
Clyde surface	50	9.0±0.7	41.0±0.7

This increase in solubility of humus material probably accounts in a measure for the growth of molds, after several wettings and dryings, on the soils that contained humus.

Chemical nature of soil colloids

During the course of the experiments in which the soil was allowed to stand with an excess of water, it was frequently observed that a colloidal material of the appearance of ferric oxide was obtained. In some cases the similarity to ferric hydrate was very marked, and in other cases the material had only a rusty stain.

It was felt that this was, in part at least, colloidal ferric hydrate, and that it was caused by bacterial decomposition of the organic matter of the soils, and solution and hydration of the released salts.

Dye-adsorption tests failed to show any significant differences. It was thought that diamine sky-blue, which had been found to be strongly adsorbed by artificially prepared colloidal ferric oxide, would show differences. It did not, however. It is very likely that the organic matter in the soil is more or less adsorbed by the ferric oxide and that it acts as a protective colloid, preventing the adsorption of an acid dye.

It was decided to try the solubility of this material in weak hydrochloric acid. Accordingly, the soils were shaken with approximately N/30 hydrochloric acid, allowed to stand for a while, and then filtered. In the filtrate iron was determined by the colorimetric method given in Bulletin 31 of the United States Bureau of Soils. The results are given in table 25:

TABLE 25. EFFECT OF DIFFERENT TREATMENTS ON THE SOLUBILITY OF IRON IN WEAK HYDROCHLORIC ACID

(Expressed in parts per million)

Soil	Soil standing in 200 per cent of water				Fresh oven-dried
	Moist	Air-dried	Oven-dried	Oven-dried and sterile	
Dunkirk surface	Trace	1.3	55.6	4.6	3.1
Clyde surface	26.6	26.4	42.75	Trace	Trace
Vergennes subsoil	Trace	Trace	Trace	Trace	Trace
Cecil subsoil	......	......	8.0	......	Trace

It is seen that oven-drying these soils previous to their standing in water increased the amount of easily soluble iron, and that sterilization

of the soils inhibited the formation of these easily soluble compounds. These results agree with the appearance of the soils.

One way to account for these effects is by bacterial activity. Some investigators have shown that oven-drying a soil increases the solubility of the organic matter but does not appreciably affect the iron compounds.

Oven-drying does not kill all bacteria. Owing to the increased food in the water with the oven-dried soil, the bacteria may work more vigorously and destroy the organic matter. Thus adsorbed iron compounds may be liberated directly, or indirectly as products of excretion. In any event, more iron compounds may be brought into solution thru bacterial destruction of the organic matter. These may hydrolyze and form colloidal ferric hydrate.

Ellis (1915) has observed this formation of ferric hydrate in many waters and has accounted for its formation by the action of special iron-bacteria. He admits, however, that the action is not limited strictly to these iron-bacteria, but that others may bring it about. It seems more reasonable to assume, therefore, that the part the bacteria play is in regard to breaking down the organic matter. This was suggested by Brown (quoted by Ellis, 1915).

That the iron compound probably first appears as crystalloidal is indicated by the manner in which it usually forms in the supernatant liquid. Its crystalloidal character was further indicated by an experiment in which some of the dried soil was placed in a collodion dialyzing sack with some distilled water, the sack then being immersed in distilled water. The colloidal precipitate was later found outside the sack as well as inside. The assumption is that part of the iron compound must have gone thru the membrane as a crystalloid and later was hydrolyzed and precipitated, for the colloidal form will not pass thru the membrane. The identity of the colloidal ferric oxide outside the membrane was established by dissolving it in weak hydrochloric acid and testing qualitatively.

SUMMARY

The experimental work here presented may be summarized as follows:

Variations of from 5 to 10 degrees between 15° and 40° C. did not materially affect the adsorption of water vapor.

The chemical composition of certain soil-forming minerals affected the adsorption of dyes. Acid dyes, as a rule, were more strongly adsorbed

by basic minerals than were basic dyes; and basic dyes were more strongly adsorbed by acid minerals.

Diamine sky-blue was one of the few dyes strongly adsorbed by colloidal ferric oxide, and, of all those examined, was adsorbed the most strongly. It was adsorbed also by alumina, but not by silica.

An alga and a fungus adsorbed considerable amounts of the dyes used in soil-adsorption work. The growth in soils of lower forms of plant life affects the adsorptive capacity of the soil.

Air-dried and oven-dried colloidal silica, alumina, ferric oxide, and humus, immersed in dye solutions, showed a reversal of their capacity to adsorb dyes. They also adsorbed water vapor rapidly.

The difference in hygroscopicity between a moist and an air-dried soil persists for three months at least.

Remoistening air-dried soils to a content of moisture above that originally held did not cause a reversal of hygroscopicity immediately, nor within three months.

Alternate wetting and drying of soils did not affect the hygroscopicity after the first drying. With the subsoils that had been wetted and dried thirty-two times there was a cumulative decrease in hygroscopicity which was significant.

Hygroscopicity was decreased successively by air-drying, oven-drying, and ignition. The change from the moist to the air-dry condition produced a greater change than that from the air-dry to the oven-dry; and from the oven-dry to the ignited condition the change was greater than from the air-dry to the oven-dry condition. Some ignited soils had comparatively high hygroscopic values.

Long immersion under water increased the hygroscopicity of a soil poor in organic matter, and decreased it in one rich in organic matter.

Leaching a soil raised its capacity for adsorbing water vapor.

Oven-drying and ignition reduced the adsorption of methylene blue. The Clyde soil, rich in organic matter, showed less effect due to drying than did the other soils. This was contrary to results with water-vapor adsorption. Effects of air-drying and alternate wetting and drying were so irregular, as measured by dye adsorption, as to be inconclusive.

Immersion of a soil in water for two years increased its adsorptive capacity for methylene blue.

Leaching a soil increased its adsorption of methylene blue.

Experiments with the adsorption of diamine sky-blue showed that less of the dye was adsorbed than of methylene blue. The only point that stood out clearly, as regards moisture changes, was that ignition decreased the adsorption of this dye.

Drying a soil decreased the amount of it that would go into suspension in distilled water and in 4-per-cent ammonium hydroxide. Drying thirty-two times as compared with drying one time decreased the amount of suspended matter.

Extractions of humus with 4-per-cent ammonium hydroxide showed no effect on humus due to drying.

Extractions with distilled water showed an increase in the solubility of the coloring matter of humus due to drying.

Oven-drying soils previous to their standing in an excess of water increased the amount of iron soluble in weak hydrochloric acid. Sterilization checked the formation of this easily soluble colloidal material.

Judged by the consistency of the results, the water-vapor-adsorption method is better than the dye-adsorption method for measuring the total surface of soils.

GENERAL CONCLUSIONS

Drying a surface soil once produces as much effect on the colloidal material as repeated dryings alternated with moistenings.

With a subsoil there is a cumulative effect due to alternate drying and wetting.

Drying a soil once or many times produces a change in the colloidal material from which it does not immediately recover on being wetted.

Drying a soil affects indirectly the reversibility of its colloidal condition, the changes being directly produced thru biological and chemical action.

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AGRICULTURAL EXPERIMENT STATION

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A STUDY OF THE PLANT LICE INJURING THE FOLIAGE AND FRUIT OF THE APPLE

ROBERT MATHESON

Three specie~ of plant lice — the green apple aphis, *Aphis pomi* De Geer (*Aphis mali* Fabricius), the rosy apple aphis, *Aphis sorbi* Kaltenbach, and the grain, oat, or apple-bud aphis, *Aphis avenae* Fabricius — are frequently very injurious to the foliage and fruit of apple. Of the three species the green apple aphis is undoubtedly the most common and widespread, doing considerable injury every year not only in bearing orchards but also in young orchards recently set and in nurseries. The greater amount of injury wrought by this species is due to the fact that it remains on the apple tree thruout the season, whereas the rosy aphis and the apple-bud aphis, or grain aphis, migrate in May, June, and early July to other host plants. In recent years the rosy aphis has also become very injurious and it now probably does as much damage in bearing orchards as does the green aphis, if not more.

DISTINGUISHING CHARACTERS OF THE THREE SPECIES OF APHIDS

The three common aphids on the apple can be readily separated in all the stages of their complicated life histories. From the standpoint of the grower it is most essential that he recognize the species as soon as they appear in the spring. The first nymphal stages of the stem mothers can be separated readily both on color markings and on structural characters. These characters may be tabulated as follows:

Species	Color	Structural characters
Aphis pomi De G	Dark apple green..........	Cornicles cylindrical, about as long as a body segment; unguis equal to one-half length of segment.
Aphis sorbi Kalt......	Dark green, with a double row of black spots down the dorsum; sides with distinct white pulverulence.	Cornicles long, cylindrical, flanged at tip; unguis distinctly twice as long as base of last segment.
Aphis avenae Fabr.....	Dark yellowish green......	Cornicles very short, tuberculate: unguis distinctly longer than one-half of segment.

The distinguishing characters mentioned in the table are well shown on Plate XVIII and in figure 111. In the field these can be seen readily with the aid of a hand lens.

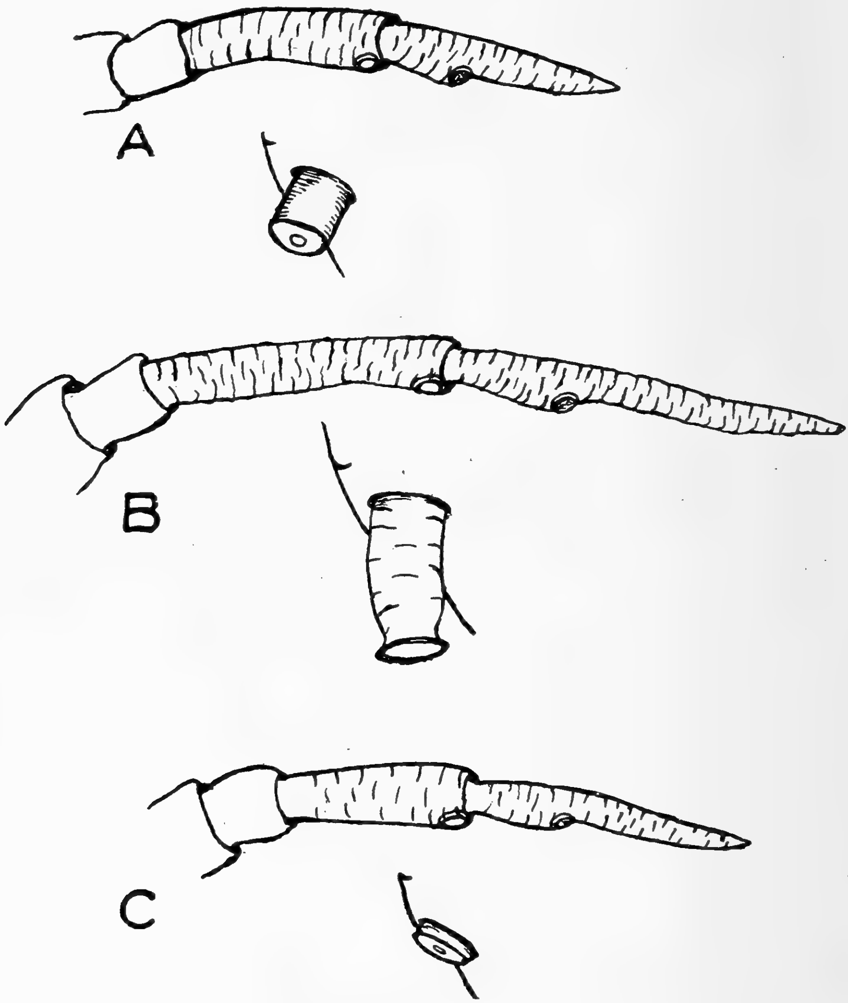


FIG. 111. ANTENNAE AND CORNICLES OF FIRST INSTAR OF STEM MOTHERS
A, *Aphis pomi*; B, *A. sorbi*; C, *A. avenae*. All drawn to same scale

The mature stem mothers are more easily separated than are the nymphs, tho the color markings vary considerably with each species. The typical forms, drawn to the same scale, are shown in Plates XIX–XXI, and the antennæ in figure 112.

Aphis pomi undergoes very slight changes in color. The mature stem mother is bright yellowish green (Plate XIX). The head is brownish,

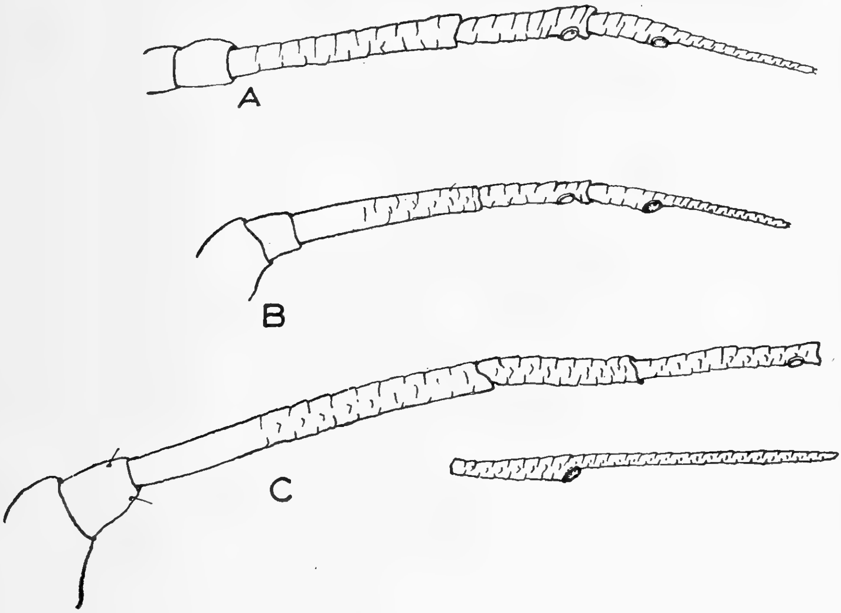


Fig. 112. antennae of mature stem mothers
A, *Aphis pomi*; B, *A. avenae*; C, *A. sorbi*. All drawn to same scale

tending toward almost black in some cases. The cornicles, the tips of the antennae, and the cauda are black, showing in marked contrast to the remainder of the body.

Aphis sorbi varies considerably in color markings. The typical form is shown in Plate XX. The color is generally a purplish brown, intermingled with greenish on the dorsum. The whole body is covered with a fine white pulverulence. There is generally a reddish brown area between the bases of the cornicles. The cornicles and the antennae, except the basal segments, are black.

Aphis avenae is very characteristic in color and is easily identified. It is yellowish green, with a dark green band extending the full length of the abdomen. This band is expanded laterally at the base of each segment, as shown in Plate XXI.

THE GREEN APPLE APHIS

(*Aphis pomi* De Geer)

SYNONYMY

The green apple aphis is a European insect. When and where it was introduced into America will in all probability never be definitely known. Unfortunately European writers have so confounded this species with the other two common plant lice of apple that it is extremely difficult, and in many cases impossible, to determine which insect is under discussion. Frequently in the same article the three well-marked species are described as if they were identical. Owing to this confusion American writers have, until recent years, failed to correctly identify the species under discussion, and the literature is in a sadly confused state. In order to clarify the situation, the following synonymical bibliography should be of considerable value:

1773 *Aphis pomi* De Geer, Mém. **3**:53, pl. 3, figs. 18–21.
1775 *Aphis mali* Fabricius, Syst. Ent., p. 737, no. 19.
1794 *Aphis mali* Fabricius, Ent. Syst. **4**:216, no. 29.
1802 *Aphis pomi* Vallot, Conc. Syst. Ouvr. Réaumur, p. 95.
1803 *Aphis mali* Fabricius, Syst. Rhyng., p. 298, no. 29.
1837 *Aphis pyri mali* Schmidberger, Köllar's Ins. Inj. Gard., For., and Farmers.
1843 *Aphis mali* Kaltenbach, Mon. Fam. Pflanzenläuse, p. 72.
1850 *Aphis mali* (in part) Walker, Ann. and Mag. Nat. Hist. 2:**5**:269.
1851 *Aphis mali* (in part) Fitch, Cat. Ins. Cab. Nat. Hist., p. 65.
1855 *Aphis mali* (in part) Fitch, Trans. N. Y. State Agr. Soc. **14**:753.
1856 *Aphis mali* Fitch, Trans. N. Y. State Agr. Soc. **16**:333.
1857 *Aphis mali* Koch, Die Pflanzenläuse, p. 107.
1863 *Aphis mali* Passeirni, Aphidae Ital.
1868 *Aphis mali* Walker, The Zoologist, p. 1297.
1871 *Aphis mali* Taschenberg, Ent. f. Gärtner und Gartenfreunde, p. 465–466.
1879 *Aphis mali* (in part) Buckton, Mon. Brit. Aphides **2**:44–50.
1880 *Aphis mali* Taschenberg, Prakt. Ins. Kunde, pt. 5:53–55.
1887 *Aphis mali* (in part) Oestlund, Syn. Aphididae Minn., p. 64.
1900 *Aphis mali* Smith, N. J. Agr. Exp. Sta., Bul. 143.
1900 *Aphis mali* Smith, Ent. News **11**:448.
1901 *Aphis padi* Sanderson, Del. Agr. Exp. Sta., Ann. Rept. **12**:191–192.
1902 *Aphis pomi* Sanderson, Del. Agr. Exp. Sta., Ann. Rept. **13**:130–136.
1904 *Aphis mali* Pergande, U. S. Div. Ent., Bul. **44**:5.

HISTORICAL

To determine when this plant louse was brought to America has been impossible because of the confused state of the literature. Due to the statements of Pergande (1904)[1] it has been generally held that the species is of recent importation. Pergande, in a careful study of *Siphocoryne* (*Aphis*) *avenae* Fabr., endeavors to clarify the synonymy of that species and concludes that it is identical with *Aphis mali* Fitch *nec* Fabricius. He states that the true European apple louse, *Aphis mali* De Geer (he surely means *Aphis pomi* De Geer, or *Aphis mali* Fabricius), was first observed by himself in the spring of 1897 and has since spread thruout the United States. That he was mistaken in his conclusions can be readily shown by a careful reading of literature.

Fitch (1855 a) in his first report has undoubtedly confused *Aphis avenae* Fabr. and *Aphis pomi* De G. This is shown in his descriptions of so many varieties, in his summary of the life history of the species, and furthermore in his published notes in the *Country Gentleman* (Fitch, 1855 b) and in his illustrations and notes in his third report (Fitch, 1856). In the *Country Gentleman* he inserts a letter from William Gilchrist, one of his correspondents, who reports on June 25, 1855, myriads of plant lice infesting his young orchard. These lice were injuring young fruit, were curling the leaves severely, and were congregated in great numbers on the tender twigs. Such are not the habits of *Aphis avenae* Fabr. (*Aphis mali* Fitch), and Dr. Fitch was puzzled, as is shown in his comments on the letter. Fitch's early observations had been confined to an infestation of *Aphis avenae* Fabr., with which were undoubtedly mingled some *Aphis pomi* De G. Evidently the injury reported by Gilchrist was caused by *Aphis sorbi* Kalt. or *Aphis pomi* De G. or by both species. In his discussion of the life history Fitch certainly outlines that of *Aphis pomi* De G. If he did not copy the life history in its entirety from European authors, he must have made some observations which warranted such an accurate description of many of the activities of *Aphis pomi* De G. Fitch also records the observations of Gilchrist that Northern Spy and Red Astrachan are not so susceptible to attack as are other varieties. This is in agreement with the recorded experience of entomologists with reference to *Aphis pomi* De G.

[1] Dates in parenthesis refer to Bibliography, page 760.

Further evidence that Fitch has undoubtedly confused *Aphis avenae* Fabr. with *Aphis pomi* De G. is seen in his third report. Figures 1 and 5 on Plate I certainly do not represent *Aphis avenae* Fabr. but are clearly illustrations of *Aphis pomi* De G. His notes also describe the work of the latter species.

It would seem to the writer that Fitch in his first detailed account confused the two species, tho undoubtedly *Aphis avenae* Fabr. was the more abundant that season and consequently Fitch's descriptions are taken from specimens of that species. However, one or more of his varieties are undoubtedly *Aphis pomi* De G., but it is difficult to definitely decide which.

If this diagnosis of the facts is correct, *Aphis pomi* De G. undoubtedly occurred in America earlier than 1854. The species doing so much injury to the young orchard of Colton (1855) in Vermont were, judging from the description of their work, probably *Aphis pomi* De G. and *Aphis sorbi* Kalt., tho it might be possible that only one species was present. Colton reports the work of these lice to have been severe since 1849. The work is certainly not that of *Aphis avenae* Fabr., and it must be concluded that either *Aphis pomi* De G. or *Aphis sorbi* Kalt. was the offender or that both species were present. This would give 1849 as the first year in which the species was recorded as doing serious injury to young apple trees in the eastern United States.

Undoubtedly the three species of plant lice, *Aphis pomi* De G., *Aphis sorbi* Kalt., and *Aphis avenae* Fabr., which are now common on apple thruout the greater part of the United States and Canada, came here from Europe in the first half of the nineteenth century. The first records of severe injury to apple are from Vermont in 1849, this injury being undoubtedly due, in part at least, to the work of *Aphis pomi* De G. Such a record would indicate that this plant louse had been present for some considerable time. Unfortunately nearly all the entomologists have confused these three species, and it is only by the most painstaking effort that it has been possible to offer the tentative synonymical table appearing on page 686. The writer feels confident that this species has been in America since the middle of the preceding century, tho it was not definitely identified until 1897.

Conclusive evidence that this species was present and widely distributed before 1897 is found in the preservation of specimens in Monell's

collection. This consists of a winged female and several young collected in St. Louis, Missouri, on July 4, 1877. Monell has the following note of this collection: "The aphids on green twigs and under side of leaves of June apple in back garden (Shaw's Garden, St. Louis, Mo.) July 4, 1877. Winged specimens under lens with abdomen green, head and thorax black; honey tubes dark; the apterous have abdomen green and thorax and head green; honey tubes black."[2]

Further evidence that the species had been present for a long time is shown by its wide distribution at the time (1897) of its first positive identification. It was found in New Jersey in 1897, in Colorado in 1898 (Professor Gillette informs the writer by letter that there are specimens in his collection bearing that date), and in Delaware in 1900.

NATURAL HISTORY

Altho the species *Aphis pomi* has been present in Europe for centuries, no very satisfactory account of its life economy can be found in European literature. While Réaumur (1734-42) mentioned plant lice as curling the leaves of apple, he gave no clear, concise description of this species or its work. De Geer (1752-78), in his remarkable Mémoires, gives a more detailed account of this species, applying to it for the first time the name *Aphis pomi.* De Geer did not confuse this species with the other two, and he presents a clear, concise account of its life history on the apple. Unfortunately this account did not attract the attention of the European entomologists, so that even to the present day the accounts of the plant lice on apple are most confused. This is all the more notable as the three common species of plant lice on the apple differ so remarkably in their life histories, their activities, and the character of their injuries to the foliage. Pergande (1904) was the first entomologist in America to clearly distinguish this species, and Smith (1900 a) was the first to present a concise account of its life history under the name *Aphis mali* Koch. Sanderson (1902) recognized that the species *Aphis mali* described by Smith is the true *Aphis pomi* De Geer. Sanderson also recognized the other two common species of apple plant lice and gave a connected account of the three species. Since the present manuscript was

[2] This information was furnished the writer by J. J. Davis, who has recently studied the Monell collection and who sent the writer the specimens referred to above.

prepared there have appeared two good biological accounts of this aphis, one by Brittain (1915 b) and the other by Baker and Turner (1916 a.)

The green apple aphis is the only species of plant lice which spends its entire life on the apple tree. This was shown by De Geer in 1773, but for some reason his interesting account remained unknown until within very recent years. The winter is passed in the egg stage. The eggs are found scattered over the succulent twigs and branches, usually in cracks or crevices or around the base of fruit spurs or leaf buds; in fact eggs may be found on almost any part of the branches when the lice are very abundant.

Hatching of the eggs

The eggs (Plate VII) hatch early in the spring, about the time when the flower buds show green at their tips or just a little later. The exact date on which the eggs began hatching at Ithaca in 1915 was April 21. This record is for eggs of this species which were laid the preceding autumn on seedling apple trees in rearing cages. These trees were kept caged all winter under normal outdoor conditions. On April 22 hatching became more general, the lice appearing in great numbers. On the 26th, large numbers of the eggs were hatching and the first cast skins were found. This continued for several days, the last eggs on this tree hatching about May 1. It will thus be seen that for this species the eggs hatch over a considerable period, at least ten days in the case of the caged trees. From observations made under orchard conditions similar conclusions were drawn, the eggs hatching during a period of at least ten days. However, the majority of the eggs hatch during the first few days, that is, at the time when the flower buds are showing green. The number of eggs hatching after the first four or five days is not very large, but this depends much on weather conditions. Sudden cold weather may delay hatching or it may destroy the young lice before they leave the eggs. In the spring of 1916 eggs were observed hatching when the blossom buds showed pink, a very important consideration when the problem of control is taken into account.

These observations are in agreement with those of other workers. Smith (1900 a) found the hatching period in New Jersey to extend over at least fifteen days (from April 15 to April 30). Gillette and Taylor (1908) state that in Colorado the eggs begin hatching before the apple

buds show green, and continue hatching for a period of two or three weeks depending on weather conditions. Brittain (1915 a) reports the remarkable observation that on different varieties of apples the eggs hatch at the time when the buds on such varieties are showing green. If such an observation should prove correct for other sections of the country, it would certainly be rather remarkable, to say the least.

Failure of the eggs to hatch

That many, in fact a very large proportion, of the eggs do not hatch, has been observed by many workers. Tho hundreds and thousands of eggs may be found on individual trees, it often happens that only comparatively few of these hatch; so that predictions as to outbreaks of plant lice cannot be made from any examination during the dormant season. Various reasons have been assigned for this failure of eggs to hatch, but none of the factors involved have been given sufficient study, particularly under experimental conditions. Unfortunately the writer has not been able, thru lack of equipment, to do more than make field observations, record the percentages of eggs that hatched, and in general correlate observed phenomena, in so far as possible, with any or all of the factors involved.

The following factors have generally been assigned as contributing to the failure of eggs to hatch:

1. Climatological conditions. These may be (1) temperature — either low temperature or sudden changes during the winter or during the hatching period; or (2) moisture — cold rains just at or just before hatching time, causing the death of the young lice before leaving the eggs.

2. Various predacious insects and birds, which may destroy or injure large numbers of the eggs during late fall, winter, and early spring.

3. Non-fertilization of the eggs. This factor, not yet mentioned by any worker, may account for the failure of many eggs to hatch. All observers agree that the males are very few, constituting a very small proportion of the total number of insects. In cage studies many females were observed to deposit eggs, thousands in fact, and tho these eggs were given the best of conditions the majority failed to hatch. It was observed also that many females deposited eggs before mating, and in a very short time shrunken eggs were noted on the twigs. Whether non-

fertilized eggs of this species will over-winter and hatch in the following spring has not been determined.

As to the proportion of the eggs that actually hatch, no very definite data can be given, as most workers content themselves with general statements. Gillette and Taylor (1908) report that in eastern Colorado not over one per cent of the eggs hatch. Brittain (1915 a) reports, in his work in Nova Scotia, 11.5 per cent hatching, and he states that other workers record as high as 30 per cent. Tho these statements refer to *Aphis pomi*, yet the eggs of *Aphis avenae* and *Aphis sorbi* must have been included, and this of course would vitiate the results. As the writer's observations were made under similar conditions it is not necessary to present them.

The stem mother

The young lice which hatch from the eggs are all females and are generally referred to as *stem mothers* (Plate XVIII). The stem mothers are wingless, viviparous females reproducing without the intervention of males. The lice, when they leave the eggs, are active creatures with long legs, capable of crawling rapidly over the limbs and branches of the trees. They settle on the green tips of the opening buds (Plate VII), and, inserting their tiny beaks, begin at once to pump out the plant juices. In company with the grain aphis they may completely cover the green tips of the buds, often as many as sixty or seventy being present on a single bud. As the buds open and as more lice hatch, their numbers increase greatly, and it is not uncommon to find every bud completely covered. With the opening of the buds the lice penetrate in among the young and tender leaves and are soon almost completely hidden among the plant hairs. The lice attack also the flower buds, frequently congregating in them in such numbers as to prevent them from unfolding. They attack also the young flower stalks, which they weaken, causing the flower to fail to develop normally.

The young lice develop rapidly provided weather conditions are favorable. As they grow they shed their skins at irregular intervals, passing thru four molts before reaching maturity. A detailed description of the stages is given below. In the writer's cages the first eggs hatched on April 21 (in 1915) and the stem mothers began producing young on May 10, a period of twenty days being required in this case for them to reach maturity. As that spring was very cold the development of the insects

was retarded. In the experiments of the preceding year the stem mothers that hatched first also required twenty days to reach maturity. Lice hatching at later dates, such as from April 26 to April 30, required from twelve to fifteen days to reach maturity, the stem mothers beginning to produce young from May 10 to May 12. In general it may be said that for the year in question (1915) the stem mothers reached maturity and began producing young from May 11 to May 14. At that time the trees were coming into full bloom and conditions were ideal for the young lice to cluster on the opening flowers as well as on the tender leaves.

Activities

After the last molt, the stem mothers become mature and begin producing young within a very short time, in many cases within twenty-four hours after the last molt or even within a shorter period. This time, however, varies greatly, apparently being dependent on weather conditions and particularly on moisture. In these experiments reproduction was delayed for several days in some instances, and several of the stem mothers died without producing any young. In the case of stem mothers placed on caged trees in the outdoor insectary, reproduction began, when the weather was clear (tho cool), usually within twenty-four hours after the last molt. Owing to the lack of necessary equipment it has been impossible to study the relation of moisture or temperature to the activities of any stages of this insect, or the effect of these factors on the predacious or parasitic enemies. General observations have been made, but it seems unwise to include them here as no accurate experimental data are at hand.

After reaching maturity the stem mothers do not move about over their host plant to any extent except when they become overcrowded or are disturbed. Under such conditions they seek new quarters and may spread generally over the tree on which they are located.

Reproductive capacity

As has already been pointed out, in 1915 reproduction was just becoming general when the apple trees were coming into full bloom. Many stem mothers, thru unknown causes, began reproducing later. Why certain stem mothers should begin reproducing considerably later than others under apparently similar conditions is unknown to the writer; tentatively several causes appear operative, but none of these have been determined

experimentally. The period of reproductive activity varies considerably, as well as the total number of young produced. This is well shown in the accompanying chart (Reproduction Chart I) illustrating the productive period and the daily rate of reproduction. On examination of the chart it may be seen that for five stem mothers the reproductive period varies from 29 to 34 days, the average daily rate of production varying from 1.38 to 2.41. The total number of young produced varied from 40 to 77. The greatest number of young produced by any one individual during a period of twenty-four hours was 10, in the case of stem mother 129. The total length of life from the time of hatching until normal death occurred varied but little, being only from 47 to 55 days in the case of the five insects reared under such conditions as to produce the normal life cycle.

From an examination of the chart it may be observed that the period of reproductive activity extends from the beginning of the blossoming period almost up to the beginning of the ordinary June drop for apples.

Description of stages

First instar (Plate XVIII).— Length 0.56–0.64 mm.; width 0.28–0.30 mm.

The newly hatched nymphs are dark green, the legs and the antennae being dark yellowish green. The eyes and the cornicles are black. On the dorsal aspect of the head are two dark chitinized areas, one on each side of the median line. The antennae are 4-jointed, with sensoria present at the distal end of the third joint and at the proximal end of the flagellum of the fourth joint.

At this stage the legs and the antennae are long as compared with the size of the body, and this gives the young lice a sprawling appearance.

This stage grows very considerably before molting, becoming elongate-oval and measuring over 0.72 mm. in length.

Second instar.— Length 0.96–1.04 mm.; width 0.48–0.50 mm.

The nymph in this stage is yellowish green, never bright nor grass-green in color. The cornicles and the cauda are black, the legs and the distal half of the antennae dusky. There are two prominent dusky patches on the head, one on each side of the median line. The antennae are 5-jointed. The cornicles are cylindrical, slightly tapering toward their tips, 0.04 mm. in length.

REPRODUCTION CHART I. APHIS POMI

Reproductive capacity of stem mother, 1915

No.	May 12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	June 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	Productive period (days)	Average daily production	Greatest number produced in one day	Total number of young	Date of death	Total length of life (days)
112	..	1	1	4	1	0	1	0	2	2	2	2	0	2	3	1	1	3	2	3	1	6	3	1	3	5	3	3	3	0	1	..	..	..	..	30	2.00	6	60	June 19	55
119	2	0	0	0	0	0	1	0	2	1	1	0	2	4	2	1	0	0	0	4	0	4	2	2	4	2	5	0	1	0	..	..	..	..	..	29	1.38	5	40	June 10	47
121	4	4	0	4	0	0	2	0	2	3	3	3	1	0	1	0	2	0	4	2	1	2	4	2	2	2	8	0	0	1	2	0	1	1	0	34	1.79	8	61	June 18	55
123	3	3	2	0	0	1	1	2	2	2	2	0	0	5	2	0	1	2	1	1	0	2	3	3	1	3	2	2	2	4	2	0	1	0	..	33	1.67	5	55	June 15	52
129	4	0	5	2	1	0	1	0	7	1	3	4	0	2	4	0	0	2	4	3	3	2	4	10	2	5	2	2	2	0	0	2	0	..	..	32	2.41	10	77	June 19	53
Averages																																				31.6	1.85		58.6		52.4

Reproductive capacity of second generation, 1915

No.	June 3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	July 1	2	Productive period (days)	Average daily production	Greatest number produced in one day	Total number of young	Date of death	Total length of life (days)
Apterous females																																				
162	..	..	..	..	..	..	1	1	1	1	5	6	3	5	4	5	5	3	1	6	2	1	1	2	2	0	1	1	1	0	23	2.52	6	58	July 9	56
163	..	..	..	..	..	..	2	0	3	2	5	7	6	3	4	5	6	3	1	2	1	1	2	1	0	0	1	1	0	1	24	2.38	7	57	July 12	56
164	..	..	..	..	..	..	..	1	4	3	4	3	5	2	4	7	2	3	4	2	1	0	0	1	2	0	0	..	..	..	18	2.67	7	48	July 2	46
134	..	2	5	5	4	6	3	0	3	2	1	1	0	2	0	0	..	..	..	..	..	..	..	..	..	..	..	..	..	..	13	2.61	6	34	June 19	36
147	..	2	3	3	6	0	2	0	0	1	1	7	4	2	2	3	1	0	0	..	..	..	..	..	..	..	..	..	..	..	16	2.31	7	37	June 20	......
Averages																															18.8	2.50		46.8		48.5
Winged females																																				
151	4	1	2	2	2	2	3	4	1	3	2	3	1	4	0	0	..	..	..	..	..	..	..	..	..	..	..	..	..	..	14	2.43	4	34	June 20	38
155	..	..	..	..	1	8	2	1	3	1	0	2	1	8	5	2	1	0	..	..	..	..	..	..	..	..	..	..	..	..	13	2.69	8	35	June 25	......
157	..	..	1	2	1	3	1	2	2	4	3	4	2	3	3	2	2	0	..	..	..	..	..	..	..	..	..	..	..	..	15	2.33	4	35	June 20	......
159	..	..	..	..	1	5	2	2	2	1	5	7	4	4	3	3	1	0	..	..	..	..	..	..	..	..	..	..	..	..	13	3.08	7	40	June 20	38
Averages																															13.7	2.63		36		38

REPRODUCTION CHART I. APHIS POMI (*continued*)

Reproductive capacity of third generation, 1915

No.	June 15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	July 1	2	3	4	5	6	7	8	9	10	11	12	Productive period (days)	Average daily production	Greatest number produced in one day	Total number of young	Date of death	Total length of life (days)
	Apterous females																																	
168	3	1	5	8	6	3	3	4	2	0	6	2	3	3	3	3	3	2	0										18	3.33	8	60	July 5	32
172				2	9	6	2	4	1	1	1	4	3	0	4	3	0	1	0	1	1								18	2.39	9	43	July 6	33
174				6	8	4	2	8	3	2	2	4	1	3	4	2	6	0	0										14	3.93	8	55	July 2	29
175				3	7	5	1	4	4	1	2	2	1	6	2	6	3	5	4	5	3	2	1	0	0	2	1	0	24	2.92	7	70	July 13	40
	Averages																												18.5	3.14		57		33.5
	Apterous forms from winged females																																	
177				6	7	4	3	7	0	3	4	1	3	0	3	2	2	2	1	1	0	0	1						20	2.50	7	50	July 16	43
178				2	9	5	5	3	2	2	4	1	7	0	6	6	4	4	6	2	3	0	2	0					20	3.65	9	73	July 17	44
179				1	0	0	5	6	1	2	6	4	1	4	5	3	2	3	3	2	4	1	2	1	0				21	2.67	6	56	July 17	44
180				4	5	8	3	6	1	0	5	1	6	2	3	2	4	4	2	0	0								16	3.50	8	56	July 4	33
	Averages																												19.2	3.08		58.8		41

Reproductive capacity of fourth generation, 1915

No.	June 22	23	24	25	26	27	28	29	30	July 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	Productive period (days)	Average daily production	Greatest number produced in one day	Total number of young	Date of death	Total length of life (days)
	Apterous females																																		
182				4	4	3	3	4	6	1	3	5	3	5	3	5	1	3	5	3	2	1	2	2	3	3	0			23	3.22	6	74	July 20	38
184			4	3	2	2	4	3	8	3	3	6	9	6	3	6	2	4	4	4	1	1	1	1	1	1	0			24	3.42	9	82	July 18	37
187	3	1	2	5	2	4	3	5	4	5	3	9	5	6	5	3	1	2	3	0	1	0								21	3.43	9	72	July 19	35
189	4	2	2	5	2	4	3	7	7	5	6	9	2	9	0	9	1	2	2	1	3	1	0	1	1	0				25	3.52	9	88	July 18	36
190			3	5	2	2	2	8	3	4	4	2	8	2	6	3	1	7	1	1	1	5	0							20	3.50	8	70	July 14	30
192	3	3	3	3	2	2	3	8	6	2	6	5	8	5	3	6	1	1	7	3	3	3	1	1	1	1	0	1	0	28	3.25	8	91	July 22	39
	Averages																													23.5	3.39		79.5		35.8
	Apterous form from winged female																																		
183	2	4	0	2	1	2	3	0	4	2	1	1	3	2	0															14	1.93	4	27	July 9	.....

REPRODUCTION CHART I. APHIS POMI (*continued*)

Reproductive capacity of fifth generation, 1915

No.	July																								Productive period (days)	Average daily production	Greatest number produced in one day	Total number of young	Date of death	Total length of life (days)
	Apterous females																													
	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28						
194	3	5	2	5	2	3	6	3	4	5	7	8	2	3	8	0	0	..	..	..	..	..	..	..	15	4.40	8	66	July 21	27
199	6	1	6	6	3	4	6	4	5	6	6	5	5	0	5	0	1	0	..	..	..	..	..	..	17	4.06	6	69	July 22	27
201	5	2	3	2	5	4	4	4	4	5	11	3	5	4	6	0	1	3	0	0	..	..	..	..	18	3.94	11	71	July 26	32
Averages																									16.7	4.13		68.7		28.7
	Apterous forms from winged females																													
204	..	2	4	0	3	3	2	2	4	3	3	10	3	0	0	..	..	..	..	..	..	..	..	..	12	3.25	10	39	July 19	25
207	..	4	3	5	2	1	3	5	2	4	7	5	4	6	4	5	1	1	2	2	4	0	1	0	22	3.23	7	71	July 29	34

Reproductive capacity of sixth generation, apterous female, 1915

No.	July																		August							Productive period (days)	Average daily production	Greatest number produced in one day	Total number of young	Date of death	Total length of life (days)
	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	1	2	3	4	5	6	7						
217	..	7	8	7	4	8	6	0	5	3	4	5	5	3	3	3	3	2	1	3	0	0	..	..	..	19	4.21	8	80	Aug. 6	33
218	1	9	6	7	5	3	4	2	0	0	3	3	2	1	0	1	4	0	0	0	..	..	..	..	..	17	3.00	9	51	Aug. 1	28
219	..	..	8	8	5	7	9	2	2	4	4	2	3	1	0	1	3	0	0	..	..	..	..	..	..	15	3.93	9	59	Aug. 1	28
220	..	..	..	..	..	5	0	2	9	1	4	5	5	5	4	5	3	8	4	5	0	1	0	1	0	19	3.53	9	67	Aug. 10	.....
221	..	10	5	7	4	2	5	2	4	2	5	6	5	0	0	..	..	..	..	..	..	..	..	..	..	12	4.75	10	57	July 27	.....
Averages																										16.4	3.88		62.8		29.7

REPRODUCTION CHART I. APHIS POMI (*continued*)

Reproductive capacity of seventh generation, apterous female, 1915

No.	July 24	25	26	27	28	29	30	31	August 1	2	3	4	5	6	7	8	9	10	11	12	13	Productive period (days)	Average daily production	Greatest number produced in one day	Total number of young	Date of death	Total length of life (days)
226	2	7	4	8	4	4	3	11	2	5	3	4	2	1	2	1	2	2	0	0	..	18	3.72	11	67	Aug. 14	31
229	2	7	5	5	3	5	3	8	2	5	3	1	2	2	0	..	..	..	..	..	..	14	3.79	8	53	Aug. 7	24
232	6	3	6	5	6	6	6	7	7	7	1	1	2	0	1	0	0	..	..	..	..	15	4.27	7	64	Aug. 9	26
236	..	2	4	1	4	4	5	4	7	4	1	4	0	1	6	5	4	1	3	0	0	18	3.33	7	60	Aug. 16	31
239	..	3	4	7	4	8	9	2	6	11	3	2	3	0	1	0	0	..	..	..	..	14	4.50	11	63	Aug. 8	25
Averages																						15.8	3.92		61.4		27.4

Reproductive capacity of eighth generation, apterous female, 1915

No.	August 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	Productive period (days)	Average daily production	Greatest number produced in one day	Total number of young	Date of death	Total length of life (days)
241	5	10	2	4	6	5	3	9	4	5	3	10	5	2	0	1	1	0	..	..	..	..	..	..	..	..	..	..	..	..	17	4.41	10	75	Aug. 22	29
243	..	8	0	3	4	3	1	1	3	3	2	1	2	3	0	0	1	2	1	1	4	0	2	2	0	0	..	..	..	..	23	2.04	8	47	Aug. 25	35
253	..	..	..	..	..	..	..	2	1	5	5	5	5	6	6	6	5	2	4	3	5	3	4	4	0	1	1	0	0	1	23	3.22	6	74	Sept. 6	.....
258	..	..	..	..	..	..	3	4	0	4	0	3	0	5	1	1	3	1	1	1	0	0	1	1	0	0	1	0	0	..	21	1.43	5	30	Sept. 1	.....
Averages																															21	2.77		56.5		32

REPRODUCTION CHART I. APHIS POMI (*continued*)

Reproductive capacity of ninth generation, apterous emale, 1915

No.	August 15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	September 1	2	3	4	5	6	7	8	9	10	Productive period (days)	Average daily production	Greatest number produced in one day	Total number of young	Date of death	Total length of life (days)
268	3	5	6	2	2	1	3	3	2	0	2	1	0	0	0	1	1	1	1	2	2	0	..	..	..	..	..	21	1.81	6	38	Sept. 5	34
272	..	6	3	1	3	2	1	4	4	6	4	1	1	2	2	4	2	1	0	1	1	0	2	2	0	..	..	23	2.30	6	53	Sept. 9	37
279	4	3	4	1	3	2	4	1	5	3	0	0	0	0	1	0	0	..	..	..	..	..	..	..	..	..	..	15	2.07	5	31	Aug. 31	29
280	3	5	3	4	1	1	1	4	0	2	2	0	0	3	1	1	0	0	..	..	..	..	..	..	..	..	..	16	1.94	5	31	Sept. 4	34
282	4	2	3	3	3	2	2	3	4	4	4	3	4	2	1	9	3	1	0	7	2	0	4	5	2	0	0	25	3.08	9	77	Sept. 8	36
Averages																												20	2.24		46		34

Reproductive capacity of tenth generation, apterous female, 1915

No.	August 24	25	26	27	28	29	30	31	September 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	Productive period (days)	Average daily production	Greatest number produced in one day	Total number of young	Date of death	Total length of life (days)
286	2	2	1	2	2	2	4	3	1	1	2	3	1	6	5	6	2	2	0	2	1	3	1	2	0	..	..	24	2.33	6	56	Sept. 17	33
288	2	4	1	2	0	0	3	3	0	1	0	1	5	3	8	2	1	6	3	3	2	3	2	0	1	0	0	25	2.24	8	56	Sept. 20	36
290	2	3	2	1	3	1	3	1	0	3	0	6	1	4	4	5	2	3	4	2	3	2	4	1	0	0	..	24	2.50	6	60	Sept. 20	36
296	..	6	1	3	3	1	3	3	0	2	3	4	1	5	6	1	4	3	3	1	0	0	..	..	..	..	..	19	2.79	6	53	Sept. 15	31
300	..	..	..	..	2	2	2	0	1	3	3	4	5	3	5	6	6	4	2	1	0	4	3	1	0	0	..	20	2.85	6	57	Oct. 6	50
301	2	3	1	0	2	2	1	2	1	0	0	0	2	4	4	4	0	0	3	3	2	0	2	2	..	..	..	24	1.67	4	40	Sept. 19	......
Averages																												22.7	2.40		53.7		37.2

REPRODUCTION CHART I. APHIS POMI (*continued*)

Reproductive capacity of eleventh generation, apterous female, 1915

No.	Sept. 3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	Oct. 1	2	3	4	5	6	Productive period (days)	Average daily production	Greatest number produced in one day	Total number of young	Date of death	Total length of life (days)
306	...	...	...	5	4	2	5	0	4	2	0	2	0	13	2	3	0	5	1	0	...	...	...	...	...	...	...	...	...	...	...	...	...	...	16	3.00	13	48	Sept. 22	29
308	...	...	2	4	4	5	6	3	2	4	4	6	2	3	7	1	0	1	1	4	0	1	0	0	0	2	0	0	0	0	0	2	0	0	30	2.13	7	64	Oct. 9	46
310	...	...	...	2	3	6	2	3	3	3	2	2	5	1	3	3	4	0	0	0	0	1	0	4	0	1	1	2	0	0	0	1	0	...	29	1.79	6	52	Oct. 8	45
311	...	...	4	3	3	5	4	3	6	2	4	4	6	3	5	1	3	0	1	0	0	0	1	0	0	0	0	1	1	0	0	...	...	...	27	2.22	6	60	Oct. 16	54
313	3	0	5	6	1	2	1	0	2	0	1	4	0	0	2	2	0	0	0	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	16	1.81	6	29	Oct. 1	39
316	...	...	...	5	4	4	5	5	4	4	5	3	5	5	6	3	2	3	2	0	2	1	0	0	0	0	2	0	0	...	...	...	...	...	24	2.92	6	70	Oct. 1	38
Averages																																			23.7	2.31		53.8		41.8

Reproductive capacity of twelfth generation, apterous female, 1915

No.	Sept. 10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	Oct. 1	2	3	4	5	6	7	Productive period (days)	Average daily production	Greatest number produced in one day	Total number of young	Date of death	Total length of life (days)
323	4	2	5	4	5	2	3	3	4	5	2	0	2	0	1	1	3	0	1	1	2	1	1	0	2	1	1	0	27	2.07	5	56	Oct. 10	42

REPRODUCTION CHART I. APHIS POMI (*concluded*)

Reproductive capacity of thirteenth generation, apterous female, 1915

No.	September															October																												Productive period (days)	Average daily production	Greatest number produced in one day	Total number of young	Date of death	Total length of life (days)
	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19															
330	8	5	5	3	3	4	1	1	0	4	0	1	1	0	1	0	1	2	2	2	3	1	2	0	0	0	3	1	0	4	1	2	0	0	*a*	..	..	..	..	..	..	..	..	44	1.52	8	67	Nov. 1	56
331	..	6	4	7	4	5	1	0	2	2	3	0	0	0	0	0	1	1	2	2	2	0	2	1	0	0	0	1	0	..	..	..	..	..	..	..	..	..	..	..	..	..	..	27	1.70	7	46	Oct. 14	39
334	2	8	9	4	3	4	1	0	0	3	3	2	0	0	1	1	1	1	5	2	1	2	0	0	0	3	0	0	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	26	2.15	9	56	Oct. 17	43
339	..	..	5	6	4	3	1	1	0	1	4	0	1	1	1	1	0	3	2	1	0	1	1	1	0	0	0	2	1	0	0	0	..	..	..	..	..	..	..	..	..	..	..	27	1.52	6	41	Oct. 19	45
340	..	8	7	4	5	3	1	1	3	1	4	0	1	1	0	0	3	2	1	0	2	1	2	0	0	1	0	2	0	0	..	..	..	..	..	..	..	..	..	..	..	..	..	27	1.96	8	53	Nov. 5	62
Averages																																												30.2	1.77		52.6		49

a 2 young on October 23, 25, and 29, respectively.

Third instar.— Length 1.28–1.30 mm.; width 0.72 mm.

In coloring and markings this instar differs but slightly from the preceding. The cauda is more prominent and the cornicles are twice as long, 0.08 mm. in length. The lateral tubercles now begin to appear on the prothoracic and abdominal segments.

Fourth instar.— Length 1.44–1.50 mm.; width 0.88 mm.

In this stage the nymph is yellowish green in color, with the legs, the distal half of the antennae, and the cauda dusky to black. The cornicles are dusky, with black at their tips. The dusky patches on the head are apparently absent. The antennae are 5-jointed. The cornicles now measure 0.16 mm. in length. The eyes are black and are now rather prominent. The lateral tubercles on the prothoracic and abdominal segments show more distinctly than in the preceding instar, and lateral tubercles appear also on the last two thoracic segments.

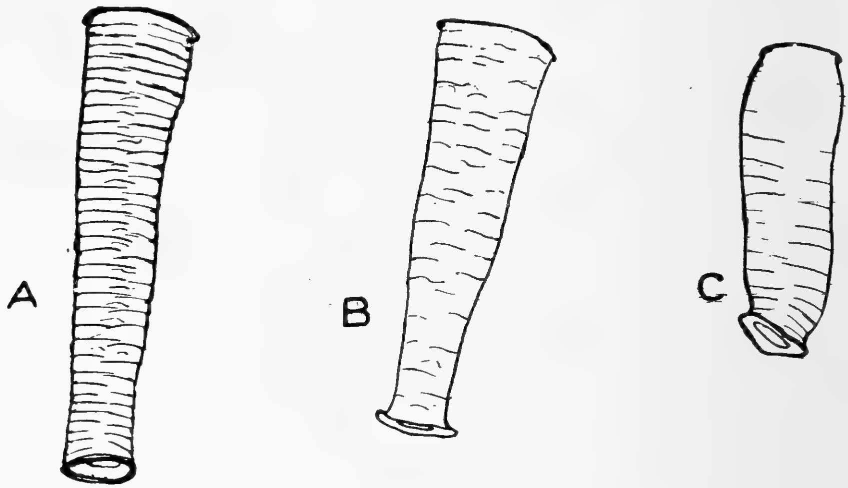


FIG. 113. CORNICLES OF MATURE STEM MOTHERS

A, *Aphis pomi*; B, *A. sorbi*; C, *A. avenae*. All drawn to same scale

Fifth instar, mature stem mother (Plate XIX).— Length 1.6–1.7 mm.; width 0.95–1 mm.

The head and the thorax are yellowish green, the head usually having a dusky appearance. The abdomen is bright to dark green, frequently mottled with yellowish green. The eyes are black and rather prominent. The cornicles are black, cylindrical, slightly tapering, 0.24 mm. long (fig. 113, A). The cauda is black, setose, prominent; the sub-

genital plate and the large oval area on the preceding segment are black. The antennae are 5-jointed, the third joint in some cases showing segmentation and thus giving a 6-jointed antenna. The length and number of sensoria of the antennal segments (fig. 112, A, page 685) are as follows: Segment III, 0.35 mm., sensoria 0; segment IV, 0.17 mm., sensoria 1; segment V, 0.11 + 0.15 mm., sensoria the usual group. The beak, reaching the base of the third pair of legs, is yellowish in color, with the last segment black. The legs are yellowish to dusky; the knees, the ends of the tibiae, and the tarsi are black. Lateral tubercles are present on the thorax and on the first eight abdominal segments.

The second generation

The young produced by the stem mothers all develop into either winged or wingless females. Fr m close observation covering two years the writer found that over 75 per cent of this generation acquire wings and rapidly distribute the species from tree to tree and from orchard to orchard. In 1915 the first individuals of this generation began maturing the last two or three days in May and the first days of June. In the rearing cages winged forms began appearing on May 31. Under the conditions of that year, which were decidedly unfavorable, the early individuals required more than nineteen days to reach maturity, while in some of the cages twenty-five days were required.

It seems rather remarkable that so many individuals of this generation are provided with wings. Various theories have been advanced to explain the production of winged forms. The one oftenest quoted is that the condition is due to crowding, resulting in the lack of food. In cage after cage in these experiments there was neither crowding nor lack of suitable food, and yet the proportion of insects that acquired wings seemed, and actually was, as large as where there was undoubted crowding. It would seem that the production of such a high proportion of winged forms in this generation is entirely a provision by the species for its rapid and widespread distribution. It is self-evident that such a provision is eminently wise, and to account for it on a basis of crowding or lack of food appears, to say the least, highly inadequate.

Activities

Wingless forms.— The wingless forms exhibit no activities differing greatly from those of the stem mothers. After reaching maturity they

migrate until a satisfactory locat on is found, usually on the underside of a leaf or on the succulent new growth. Here they may congregate in considerable numbers, insert their beaks into the leaves, and, as they feed, bring forth their young. Once located they seldom move except when disturbed or when crowding becomes excessive, when they may be observed searching out new feeding places.

Winged forms.— The activities of the winged forms are much more varied and are of considerable significance for the species. The insects appear very excitable, and when disturbed they move about actively or readily take to flight. They do not settle permanently in any one place, but feed for shorter or longer periods on either the leaves or the succulent young growths. They deposit their young from time to time, and the species is distributed very rapidly during the early days of June. Frequently, if the stem mothers have been fairly abundant, considerable flights of the winged forms may be observed in the early days of June; and it is not at all uncommon at that time to find practically all the lower and outer leaves of trees that had previously been free of lice with two or three winged lice on each leaf.

Reproductive capacity

Wingless forms.— In the writer's rearing work, the reproductive capacity of the wingless forms was not so great as that of the stem mothers. This may be seen by consulting the chart, the reproductive capacity of five individuals varying from 34 to 58. The period of reproduction is considerably shorter than that of the stem mothers, and the daily rate of production is much higher.

Winged forms.— In the winged foims the number of young produced averages less than in the wingless forms, the productive period is shorter, and the average daily rate is about the same. In the case of the winged forms it was rather difficult to obtain accurate results, owing to the wandering habits of the insects and the fact that the cages, tho of considerable size, did not seem to allow normal development. From such considerations the writer is inclined to believe that the reproductive capacity shown in the experiments is too low.

Both forms.— From all the cage records, the total length of life of the apterous forms of this generation appears to be about the same as that of the stem mothers, whereas the winged forms have a considerably shorter life. Field observations have confirmed the cage experiments in this regard.

In comparing the reproductive capacity of this generation with that of the stem mothers, it will be observed that the period of reproductive activity is shorter, the average daily number of young produced is greater, and the total number of young is less. The total length of life is considerably shorter.

Description of stages

No attempt is made in this or in the following generations to describe the nymphal stages. Only the mature forms of each generation are described.

Apterous female, second generation.— In color markings, form, and size, this insect does not differ in any material respect from the apterous female of the third generation, which is described in detail on page 708.

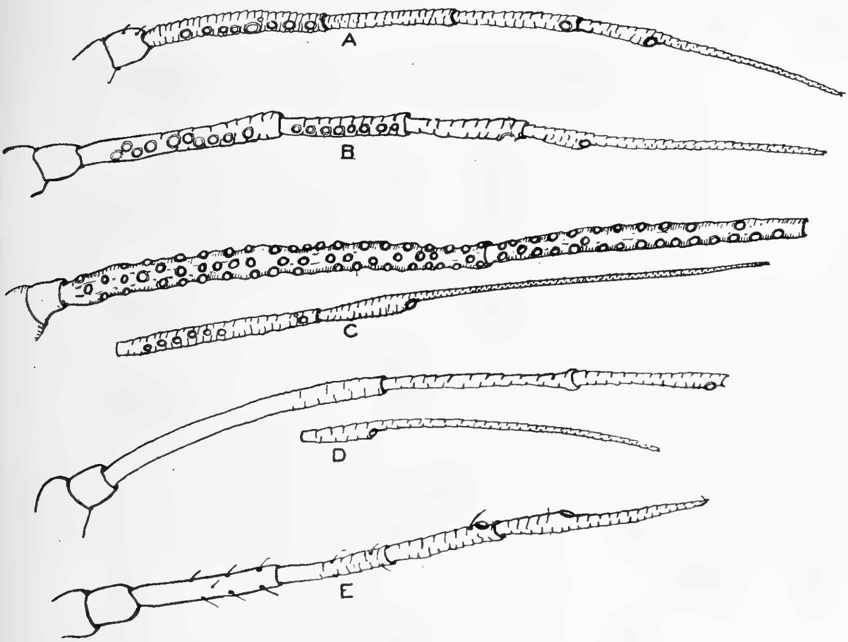


FIG. 114. ANTENNAE OF VARIOUS FORMS

A, *Aphis pomi*, winged viviparous female; B, *A. avenae*, spring migrant; C, *A. sorbi*, spring migrant; D, *A. sorbi*, apterous female on plantain E, *A. pomi*, apterous female, summer form

Winged viviparous female, second generation.— Length 1.6–1.8 mm.; width 0.72–0.80 mm.; cornicles 0.28–0.32 mm. long. (The cornicles vary somewhat in length, but the majority are 0.32 mm. long.)

The abdomen is green, occasionally tinged with yellow, with three or four dusky patches on each side in front of the cornicles; the head, the thorax above and below, the cornicles, the cauda, the genital plates, the tarsi, and the distal ends of the tibiae and the femora, are black or blackish; the prothorax is margined in front and behind with green; dusky to black dorsal median patches on the sixth, seventh, and eighth abdominal segments are usually present. Lateral tubercles are present on the prothorax and on most of the abdominal segments. The eyes are a very dark red, usually appearing black, with a small posterior tubercle and with three ocelli appearing as yellow-tipped elevations. The antennae are 6-jointed; the basal two and the last two segments are dusky to blackish, the others yellowish (fig. 114, A). The cornicles are cylindrical, gradually tapering toward the distal end, with a small, well-defined flange (fig. 115, A).

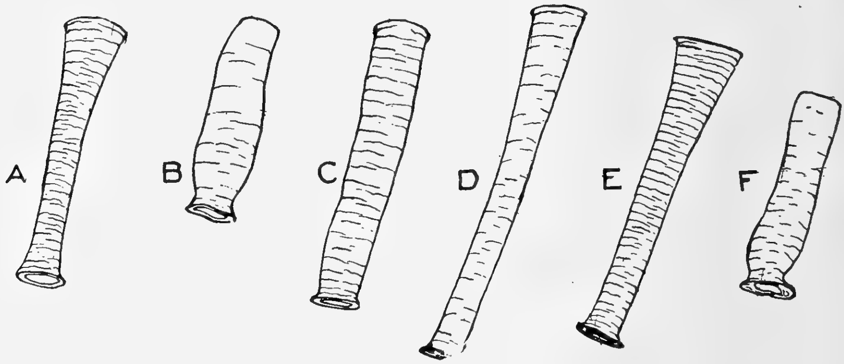


FIG. 115. CORNICLES OF VARIOUS FORMS

A, *Aphis pomi*, winged female, second generation, B, *A. avenae*, spring migrant; C, *A. sorbi*, spring migrant; D, *A. sorbi*, apterous female on plantain; E, *A. sorbi*, fall migrant; F, *A. avenae*, fall migrant. All drawn to same scale

The third generation

As is well known, all the summer generations of this plant louse consist of viviparous females, reproducing without the intervention of males.

In the case of the second generation, a majority, over 75 per cent, were found by the writer to be winged females. In the third generation the majority are wingless, less than 50 per cent possessing wings. This number, however, greatly aids in the rapid dispersal of the species, and this dispersal becomes very marked during the first half of June. The winged forms from the stem mothers reach their maximum numbers at that time, and are followed closely by the winged forms descended from the second generation.

In the outdoor cages the second generation began producing young on the last day or two of May and the third generation began maturing on June 12. On June 13 the wingless females of the third generation began producing young. Production of young by this generation became general about June 20.

Activities

The activities and habits of this generation do not differ in any marked degree from those of the preceding. However, the damage they do is more consequential. The third generation and its young congregate not only on the leaves, causing them to curl considerably, but also on the rapidly growing shoots, the fruit stems, and the fruits themselves. Usually the insects are found in company with the rosy aphis, so that from general observations one cannot state how much of the leaf curling is due to the one or to the other species. In general it may be stated that the green apple aphis (*Aphis pomi*) does not cause the leaves to curl so badly, but is a worse pest of the tender shoots (Plate VII), causing them to die in many cases and stunting them in others. It also dwarfs the young apples, making them knotty and gnarled and preventing much of the ordinary June drop — resulting in cluster fruits, so common to the orchardist. In this last type of injury, however, the rosy aphis is the worst offender, tho the green apple aphis when abundant is a serious factor in this work.

Reproductive capacity

Unfortunately, thru a mistake in the writer's cage work, the reproductive capacity of only the wingless forms was determined. However, there is shown in the table (Reproduction Chart I) the reproduction of wingless descendants of winged forms of the second generation and of descendants

of the wingless forms. The descendants of winged forms are indicated separately in the reproduction chart.

On consulting the table it may be seen that the average productive period is nearly identical with that of the wingless forms of the second generation. The daily production of young is much higher, on the average, and the total production is almost equal to that of the stem mothers. The length of life, however, is considerably shorter, more nearly approaching that of the winged forms of the second generation.

Description of stages

Adult apterous female, third generation.—Length 1.7–2 mm.; width 1 mm.; cornicles 0.4 mm. long.

The general shape is pyriform. The color is light green to bright yellowish green; the head is yellowish, often shading to dusky yellow. The eyes are dark red, appearing almost black. The antennae are yellowish, with the distal half dusky. The distal ends of the femora, the tibiae, and the tarsi are black. The cornicles are cylindrical, black, gradually tapering, with a distinct flange at the distal end. The cauda and the genital plate are black. Lateral tubercles are present on the prothorax and on the abdominal segments.

Adult winged female, third generation (Plate XXII).—The winged female of the third generation does not differ in any respect from that of the second generation and requires no separate description.

The fourth generation

At Ithaca the first individuals of the fourth generation reached maturity and began producing young on June 21. The production of young by this generation became more or less general about the last of June. The habits and activities of this and succeeding generations do not differ from those of the third generation and need not be discussed in any further detail.

The reproductive capacity of the fourth generation presents some interesting features. The period of reproduction is longer than that of either the second or the third generation, and the daily number produced by each individual is considerably greater. The total average production is much higher than for any preceding generation.

Succeeding generations

The generations of *Aphis pomi* follow one another with great regularity and rapidity. This succession may be easily grasped by examining the chart (Reproduction Chart I) and figure 116. Each generation after the first of June matured in from eight to twelve days, the maximum period being for the eighth generation, during the last of July, and the tenth generation, in the latter half of August.

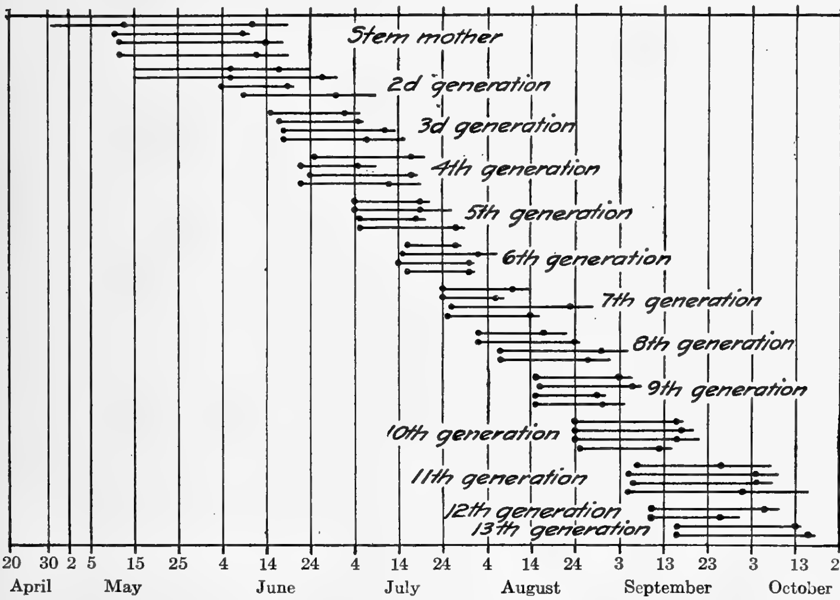


FIG. 116. GENERATIONS OF APHIS POMI

The part of the line between the round dots represents the productive period; the remainder of the line represents the period of life after production ceased

The habits and activities of these later generations present no great variations from those already discussed. Altho reproduction continues at a very high rate and there are many overlapping generations, yet the activities of the many predacious and parasitic enemies of the insects usually hold them fairly well in check. However, severe outbreaks have occurred and may be expected to continue to occur at any period during the summer. The detailed report and discussion of the parasitic and

predacious enemies of apple plant lice are deferred until a future time, in order to bring together more data and present them in a thoroly digested form.

Number of generations

During the season of 1915 there developed in the outdoor breeding cages fourteen viviparous generations. The fifteenth generation consisted of true males and females. This generation reached maturity about October 1. Mating began on that date and the first egg deposition was observed on October 4. Egg deposition began in the neighboring orchards at the same time.

Altho in the rearing-cage work the generation maturing on October 1 proved to consist of true males and females, yet for more than a month after that time viviparous females were producing young in the field under exactly similar conditions to those in the rearing cages. This would indicate that generations starting from young deposited by the stem mothers during the early part of June (as shown in the chart) do not begin producing the male-and-female generation until later in the fall. However, as to the average number of generations in a single season, no definite figure can be given without rearing thru a very large series, starting with the earliest- and latest-maturing stem mothers. This would involve too much detailed labor without adding materially to the knowledge of the subject. Judging from rearing work and field observations, the writer is led to conclude that in all probability there are ten full generations or more in a single season. When one considers the great reproductive capacity of each of these generations, it is not to be wondered at that severe infestations may occur at any time provided the natural checks are interfered with in any way.

Reproductive capacity of Aphis pomi

In consulting the reproductive capacity chart, some interesting facts may be observed. The maximum productive period (31.6 days) is for the stem mothers, and the thirteenth generation follows closely with 30.2 days. Unfortunately, no data were obtained on the fourteenth generation, owing to the death of the viviparous mothers in the special rearing cages. The minimum productive period (13.7 days) occurred only with the winged females of the second generation. The productive period varied

considerably for the other generations, tho in general it became shorter during the warmer part of the summer.

The fourth generation produced the maximum average number of young (79.5), tho not at the maximum average daily production. The minimum average number of young (36) was produced by the winged females of the second generation. The average daily production is very interesting. It gradually increased from 1.85 in the case of stem mothers to 4.13 for the fifth generation, and then gradually declined to 1.77 for the thirteenth generation.

The male-and-female-producing generation

In the rearing cages the fourteenth generation proved to be the male-and-female-producing generation. In their habits and activities the apterous viviparous females of this generation do not differ in any marked degree from the ordinary summer generations. They are sluggish, not showing any wandering propensities but depositing their young with quiet regularity. Owing to a series of accidents no complete records of the reproductive capacity of this generation were obtained. This is unfortunate, for such information would be highly instructive.

Description of mature apterous female, fourteenth generation

Length 1.92–2 mm.; width 1.04–1.2 mm.; cornicles 0.4 mm. long.

The abdomen is dark green, with yellowish brown lines often forming a somewhat reticulate pattern on the dorsal surface; the head and the thorax are yellowish brown; the distal ends of the femora, the tibiae, and the antennae, and the tarsi, the cauda, and the cornicles, are black. The cornicles are cylindrical, and are tapering and slightly flanged at their tips.

The oviparous females and the males

The oviparous females and the males of *Aphis pomi* are very easily distinguished from individuals of the viviparous generations. They are wingless, are much smaller than the other generations, differ considerably in their general color, and show marked differences in their habits.

In 1915 the oviparous females first reached maturity on October 1 and egg deposition began on October 4 in the rearing cages. In 1914 egg laying was first observed on October 6; in the field eggs were first observed a few days later. The egg-laying forms are active and do not

remain permanently in any one place. They may feed for a short time and then move about, locating a new place to obtain food or migrating to the twigs and depositing eggs. After each egg deposition the female returns to feed, and several days are usually occupied in the important process of egg laying. During all this time the few males that may be present actively mate with the females. In general, however, it may be said that only a small number of the females ever become fertilized, owing to the small number of males. Whether such non-fertilized eggs ever hatch has not been determined for this species, so far as is known.

As to the number of eggs that a single female is capable of laying, no definite statements can be found in literature, each author contenting himself with the barren remark that a few are laid. In the fall of 1914 a large number of experiments were conducted under normal outdoor conditions to determine this point. At the same time many dissections were made to confirm or deny the conclusions drawn from such experiments.

The table on the following page shows in a graphic form the principal data obtained.

From the table it is seen that the number of eggs laid varies considerably. Altho many females were experimented with, only a few seemed to act in a perfectly natural manner. Furthermore, it was difficult to obtain nearly mature females that had not deposited eggs, and then find a sufficient number of males, without more extensive rearings than could be made under the prevailing conditions. It would appear, from the experimenting done, that in order to secure perfectly natural conditions it is necessary to include a male in each rearing cage.

The egg-laying period extends over a considerable time. In 1914 the first eggs were deposited on October 6 and deposition continued to as late as December 1. The maximum egg deposition was reached about the latter part of October, yet many eggs were laid late in November. On November 17, 1914, a severe frost apparently froze all the females in the rearing cages. But when some of these were brought into the laboratory they revived and became active; while many of those left out of doors gradually revived, and active females were found as late as December 1. In 1915 egg deposition began on October 4, reached its maximum the latter part of the month, and continued intermittently until the end of November.

Experiment no.	Number of lice	Date when experiment was started	Number of eggs laid: October 16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	November 1	2	3	4	5	6	7	8	9	10	11	12	13	14	Total number of eggs laid
1	1 ♀	Oct. 16		1		1		1				♀ dead																					3
2	1 ♀	Oct. 16			1	♀ missing																											1
3	1 ♀	Oct. 16			1							♀ dead (quietly feeding up to day of its death)																					1
4	4 ♀	Oct. 16		5			4	4				♀ all dead																					13
6	1 ♀	Oct. 16		1		2		1				♀ dead																					4
7	1 ♂, 1 ♀	Oct. 21												1						1											♀ dead		2
8	1 ♂, 1 ♀	Oct. 21										1								2			♀ dead										3
9	1 ♂, 1 ♀	Oct. 21										2								1	♀ nearly dead		♀ dead										3
10	1 ♂, 1 ♀	Oct. 21																		1			2								2	♀ missing	5

The males are very few in number, comprising scarcely one per cent of the sexual generation. In many of the rearing cages, scarcely more than two or three males could be found among at least four to five hundred individuals. The few males present are always active, running about with great agility and mating with the females indiscriminately. Because of the very small number of males, undoubtedly hundreds and thousands of females are never fertilized.

The oviparous female (Plate XXIII)

Length 1.48–1.6 mm.; width 0.88 mm.; cornicles 0.32 mm. long.

The oviparous females are wingless and are regularly oval in outline. They are variable in color, but are usually yellowish green tho dark green specimens are not uncommon and very frequently practically all the green

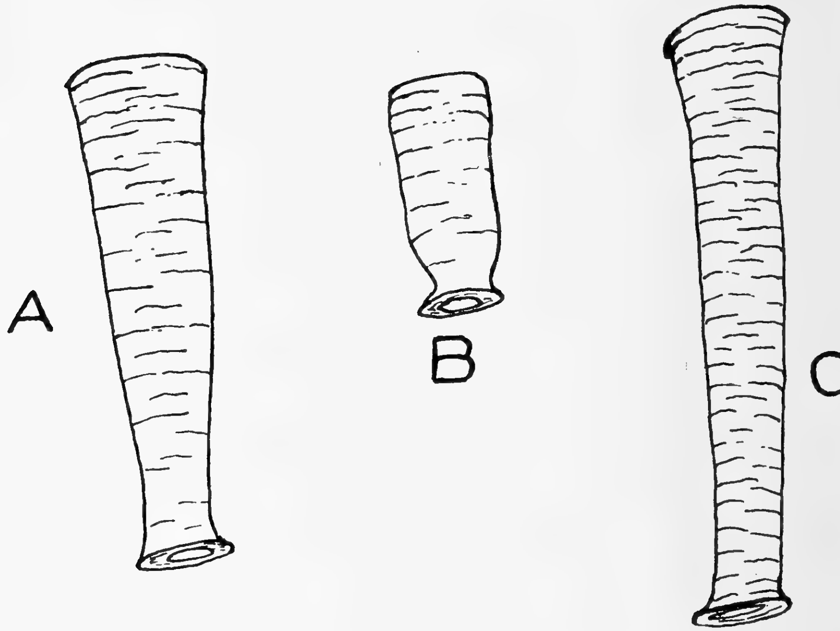


FIG. 117. CORNICLES OF VARIOUS FORMS

A, *Aphis pomi*, oviparous female; B, *A. avenae*, oviparous female; C, *A. sorbi*, oviparous female. All drawn to same scale

is lacking and the lice are from bright rusty yellow to yellow in color. Dark spots scattered over the dorsum of the abdomen are not uncommon. The head is dusky brown to yellowish; the distal half of the antenna is dusky to black, the proximal part is yellow; the legs are yellowish, with the distal ends of the femora, the tibiae, and the tarsi black; the cornicles (fig. 117, A) are black, cylindrical, gradually tapering toward their distal

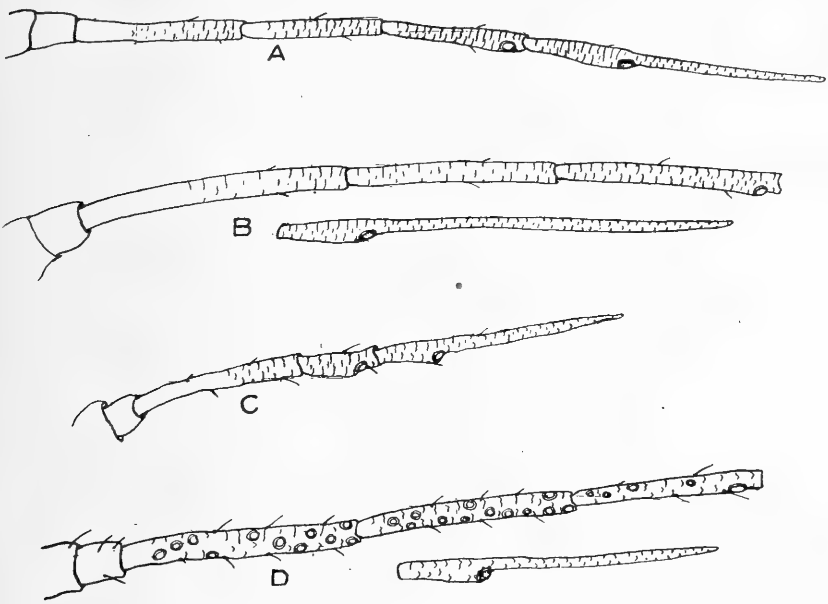


FIG. 118. ANTENNAE OF VARIOUS FORMS
A, *Aphis pomi*, oviparous female; B, *A. sorbi*, oviparous female; C, *A. avenae*, oviparous fema. D, *A. pomi*, male. All drawn to same scale.

ends, which are slightly flanged; the cauda is prominent and black; the segment directly in front of the subgenital plate is marked with two prominent oval black spots, one on each side of the median line. The length and number of sensoria of the antennal segments (fig. 118, A) are as follows: Segment III, 0.22 mm., sensoria 0; Segment IV, 0.15 mm. sensoria 0; Segment V, 0.16 mm., sensoria 1; Segment VI, 0.8+0.23 mm., sensoria the usual group.

The oviparous female is particularly distinguished from the females of the other generations by the position of the sensoria on the antennae and their presence on the hind tibiae. These are shown in figures 118, A, and 119, A.

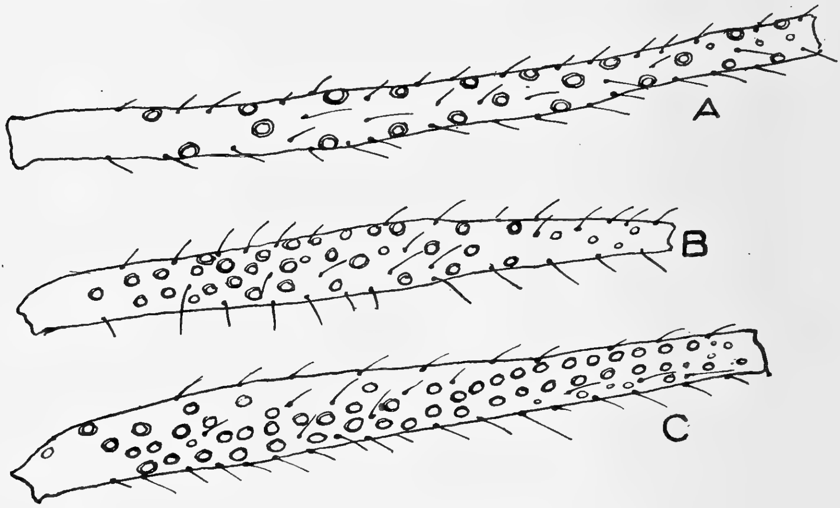


FIG. 119. HIND TIBIAE OF OVIPAROUS FEMALES
A, *Aphis pomi*; B, *A. avena* ; C, *A. sorbi*. All drawn to same scale

The male (Plate XXIII)

Length 0.96–1.2 mm.; width 0.48–0.56 mm.; cornicles 0.16 mm. long.

The males are wingless. The general color is brownish yellow; the head and the antennae are dusky to black; the cornicles, the cauda, and the genitalia are black; the distal ends of the femora, the tibiae, and the tarsi are dusky to black. The cornicles are cylindrical, slightly tapering toward their distal ends, with a slight flange-like expansion at their tips. The antennae are 6-jointed, nearly equaling the length of the body. The sensoria are as shown in figure 118 D. The length of the antennal segments and the number of sensoria of each are as follows: Segment III, 0.23 mm., sensoria 8–12; Segment IV, 0.22 mm., sensoria 8–11; Segment V, 0.2 mm., sensoria 3; Segment VI, 0.09+0.24 mm., sensoria the usual group.

The egg

The egg is oval in form, slightly flattened on the side next the bark. The length is from 0.48 to 0.56 mm. When first laid it is bright yellow

in color, and is covered with a glutinous substance which hardens with age. The color gradually changes to greenish yellow and finally to a shining jet-black. The time required for this change in color varies under normal outdoor conditions from about nine days to more than two weeks.

The production of winged forms

In the case of *Aphis pomi* the production of winged forms is for one purpose only; this is distribution, not migration to different host plants. For this purpose it is essential that the early generations should provide a very high proportion of winged forms, so that advantage can be taken of the large numbers and widespread occurrence of the host plant (apple). This is exactly what takes place in nature, over 75 per cent of the second generation and between 25 and 50 per cent of the third generation acquiring wings. Such a large proportion of winged forms so early in the season insures a widespread distribution and does not call for any marked production of winged forms thruout the summer; and such a condition appears to be the normal one for this species. Smith (1900 a) states that no winged forms are produced after the third generation. Sanderson (1902) and Gillette (1908) report winged forms occasionally appearing as late as the last of August. In the rearing-cage work practically every generation produced a few winged forms. In the fourth generation very few winged forms appeared, but fully 50 per cent of the fifth generation were winged. In all other generations except the ninth, the thirteenth, and the fourteenth, a few winged forms appeared. In the field winged forms were not uncommonly found during July and August, while in 1915 in the cages the last winged forms appeared on September 6. This would seem to indicate that practically all the generations during any season do and can produce winged forms. Whether the direct descendants of the winged forms may also be winged has not been positively determined for all generations. In all cases studied so far, the first generation from winged ancestry are always wingless, whereas the second generation may be either winged or wingless. Should this prove true for all winged individuals, the results would agree with those found by Professor Slingerland in his extensive studies of *Aphis avenae*.[3]

[3] Manuscript notes by Professor Slingerland.

Many opinions have been offered by various workers on the causes or factors that influence the production of winged forms in aphids. So far all these offerings are mere opinions, one of the most favored being the crowding of the insects on the food plant and the consequent reduction of the food supply. In all the writer's work of rearing thousands of individuals, crowding was eliminated and yet the percentage of winged forms for any one generation did not seem to vary. The question of the production of winged forms in aphids is one deserving deeper study than has yet been devoted to it, and the results might prove of great economic importance.

Food plants

The green apple aphis is very restricted in its host plants, being confined to a few very closely related forms. The author has found the species on the following food plants: apple (*Pyrus malus* L.), pear (*Pyrus communis* L.), American crab (*Pyrus coronaria* L.), mountain ash (*Pyrus americana* Marsh and *P. aucuparia* L.), hawthorn (*Crataegus oxyacantha* L. and other species of Crataegus), and quince (*Cydonia* spp.).

Of these food plants the apple is the one most generally attacked and injured. Some varieties of apples are more susceptible than others, and from the writer's observations the following appear to be the most susceptible to injury: Twenty Ounce, Maiden Blush, King, Fall Pippin, Greening, and Baldwin.

THE ROSY APPLE APHIS

(*Aphis sorbi* Kaltenbach)

Altho the species *Aphis sorbi* was recognized at an early date (1854) by Fitch under the name *Aphis malifoliae*, yet, like *Aphis pomi* and *Aphis avenae*, it has been and still is greatly confused in the literature. Its characteristic work on the apple, and its bionomics, are very different from those of either of the other two species named, and had a serious study been made of its life economy all this confusion would have been avoided. Recently two rather extensive papers on the species have been published, so that its work, life history, and distribution are now becoming well known. The present paper is based on extensive rearing experiments made at Ithaca during the seasons of 1914, 1915, and 1916, and the manuscript was practically completed before the publication of the reports of Brittain (1915 b) and Baker and Turner (1916 b).

SYNONYMY

The synonymy of *Aphis sorbi* is in a rather chaotic condition. Since Sanderson's work in 1901 and 1902, the species has been generally known as *Aphis sorbi* Kaltenbach, altho a few workers have doubted the correctness of this view. Recently Baker and Turner (1916 b), after an examination of European specimens of *Aphis sorbi* taken on *Sorbus* spp. in the same region as the original material, concluded that the American species is distinct and should be known as *Aphis malifoliae* Fitch. Their conclusions do not seem to the writer to be well founded. They admit the almost exact identity of the European and American specimens, both in color markings and in morphological characters. The only characters they use in making their separation in the wingless forms are the relative lengths of the cornicles and antennal segments, and the size of the lateral tubercles. In the winged forms the only characters used are the relative lengths of the antennal segments. In support of these views Baker and Turner give two tables of measurements, one of four individuals and the other of six, taken at random. These tables show a relatively small, tho apparently definite, variation in length. However, on consulting the body of the work the variation in the lengths of these same characters is found to be much greater and to overlap very considerably for the two species. Before these characters can be given weight, it should be shown that in a long series of measurements the means for *Aphis sorbi* Kalt. and *Aphis malifoliae* Fitch are distinct and do not completely overlap. Furthermore, the lengths of antennal segments and cornicles in aphids have, to say the least, been shown to be poor morphological characters on which to base specific determinations, unless coupled with other marked differences.

From a careful reading of the literature and from the considerations just mentioned, the author is not prepared to accept the conclusions of Baker and Turner.

Recently Theobald (1916) also has attempted to untangle the synonymy of this species, and he concludes that it should be known as *Aphis kochii* Schouteden. *Aphis kochii* was the name given by Schouteden (1903) to *Aphis pyri* Koch, as the name *pyri* had already been preoccupied by Boyer de Fonscolombe (1841). Koch's (1854–57) description of this species does not agree with the species *Aphis sorbi* Kalt., and the writer is convinced that the latter should stand as a distinct species, for the

present at least. However, Theobald's description undoubtedly refers to *Aphis sorbi* Kalt., not *Aphis kochii* Schouteden (*Aphis pyri* Koch).

The following table presents what the writer considers the synonymy of this species:

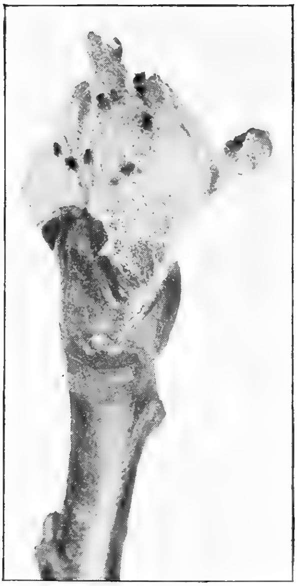
Aphis sorbi Kaltenbach
Aphis pyri Boyer of Koch, not *Aphis pyri* Boyer
Aphis malifoliae Fitch
Aphis kochii Schouteden of Theobald, not *Aphis kochii* Schouteden
Aphis pyri Boyer of Gillette and Taylor, not *Aphis pyri* Boyer

HISTORICAL

The rosy apple aphis is a European species which was introduced into America at an early date; when or where this introduction took place cannot be determined because of the confusion in literature of the three species now known to be common on apple. Very little is known of the history of this species in America, and because of the meagerness of references and descriptions it seems impossible to do more than summarize the situation.

Fitch (1855 a) first described what is undoubtedly the winged fall migrant of this species under the name *Aphis malifoliae*. The material on which his description was based was collected on apple leaves in Mercer County, Illinois, on October 4, 1854. Thomas (1879) considers Fitch's species as valid, and presents a description copied largely from the original. However, he adds his own observations and concludes that this species is as common and widespread in southern Illinois as is *Aphis mali* Fabr. (this includes *Aphis pomi* De G. and *Aphis avenae* Fabr.). The next positive reference to this species is by Comstock (1894). His reference to *Aphis sorbi* is given with a question mark. However, thru the kindness of J. J. Davis, who has recently examined the Monell collection, the writer can state that the species to which Comstock referred is *Aphis sorbi* Kalt. Mr. Davis found specimens of this species sent by M. V. Slingerland in September, 1893, to Monell, and Comstock's reference is certainly to this material.

Lugger (1900) refers to this species and presents figures illustrating the insect and its work, but does not state that he found it in Minnesota. The first real work on the bionomics of this species was by Sanderson (1901 and 1902). Since that time various short articles have appeared in widely separated parts of the United States, the only detailed accounts



YOUNG STEM MOTHERS ON AN OPENING BUD. MAGNIFIED

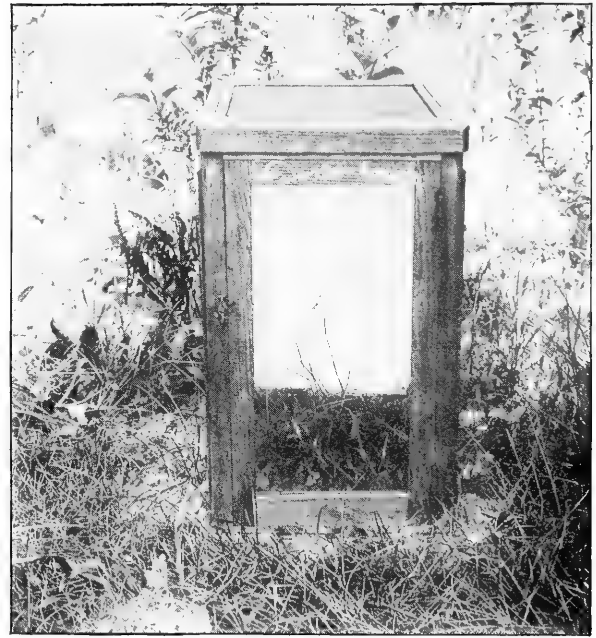
EGGS OF APHIS POMI, A. SORBI, AND A. AVENAE. MAGNIFIED

APHIS POMI CLUSTERED ON A TENDER APPLE SHOOT

CAGE ENCLOSED WITH CHEESECLOTH, IN WHICH ARE GROWING A SEEDLING APPLE AND NARROW- AND BROAD-LEAVED PLANTAINS

SPRING MIGRANTS OF APHIS SORBI ON A LEAF OF NARROW-LEAVED PLANTAIN

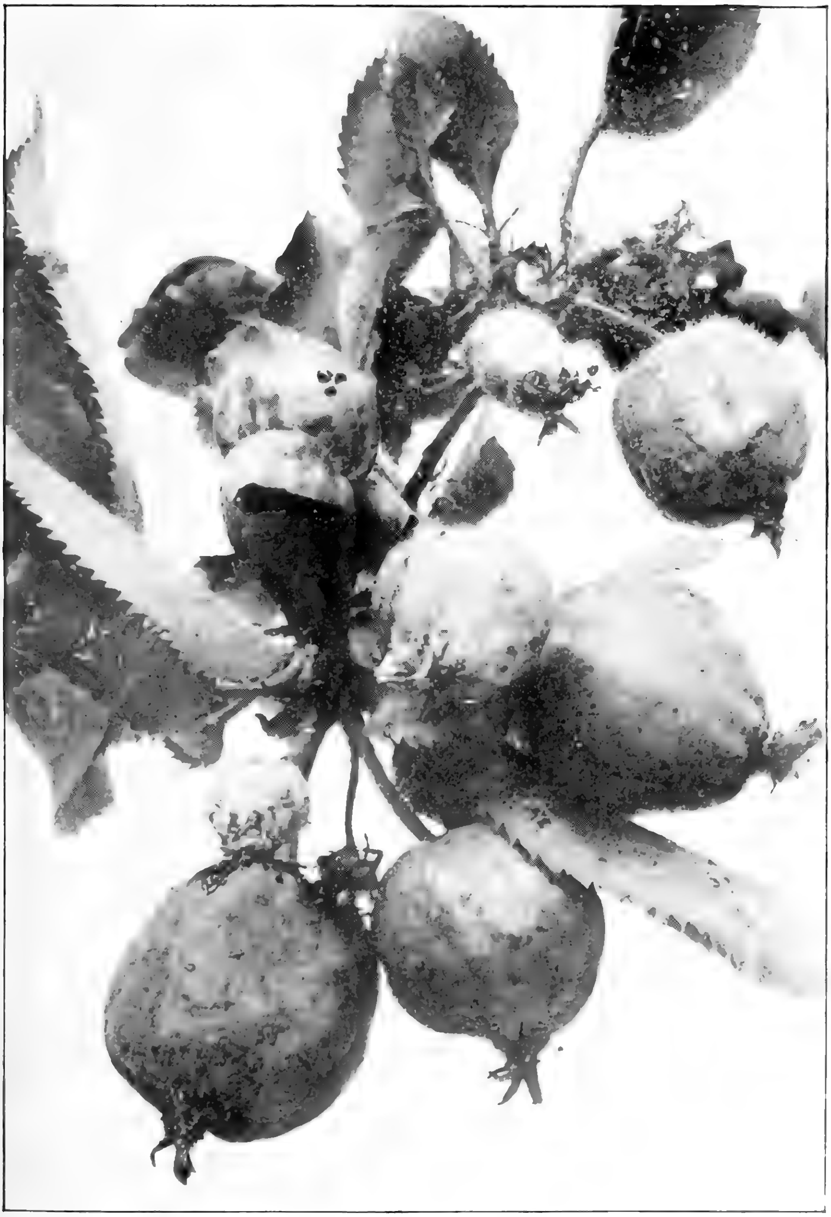
A NARROW-LEAVED PLANTAIN HEAVILY INFESTED WITH APHIS SORBI



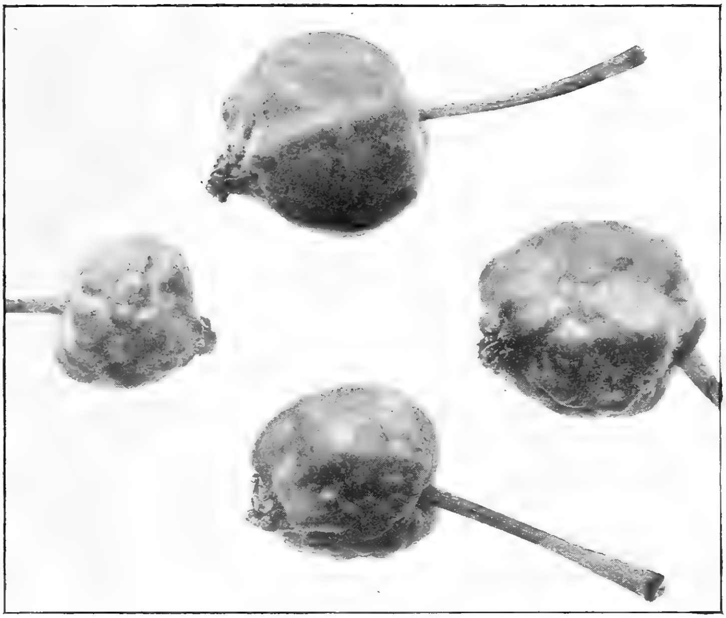
THE SAME PLANTAIN KILLED BY APHIS SORBI

VIGOROUS SHOOTS OF CRATAEGUS MONOGYNA ATTACKED BY APHIS POMI IN MIDSUMMER (JULY 19, 1918), SHOWING CURLING OF FOLIAGE

APHIS POMI SWARMING ON YOUNG TOMPKINS KING APPLES



APHIS POMI CLUSTERING ON LEAVES, FRUITSTALKS, AND FRUIT OF TOMPKINS KING APPLES (JULY 1). NATURAL SIZE



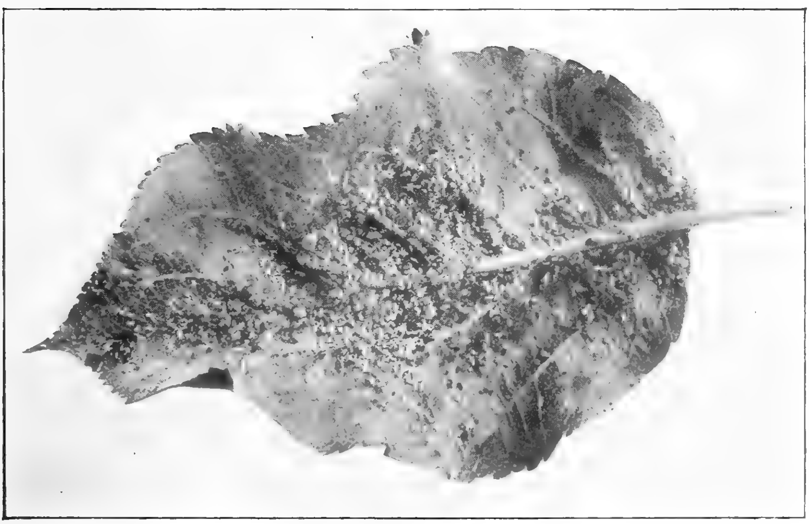
TOMPKINS KING APPLES SEVERELY INJURED BY APHIS POMI (JULY 4)

"CLUSTER FRUITS," OR "APHIS APPLES"

APHIS SORBI READY TO ATTACK THE FRUITS OF TWENTY OUNCE APPLES, AFTER SEVERELY CURLING THE LEAVES (MAY 31)

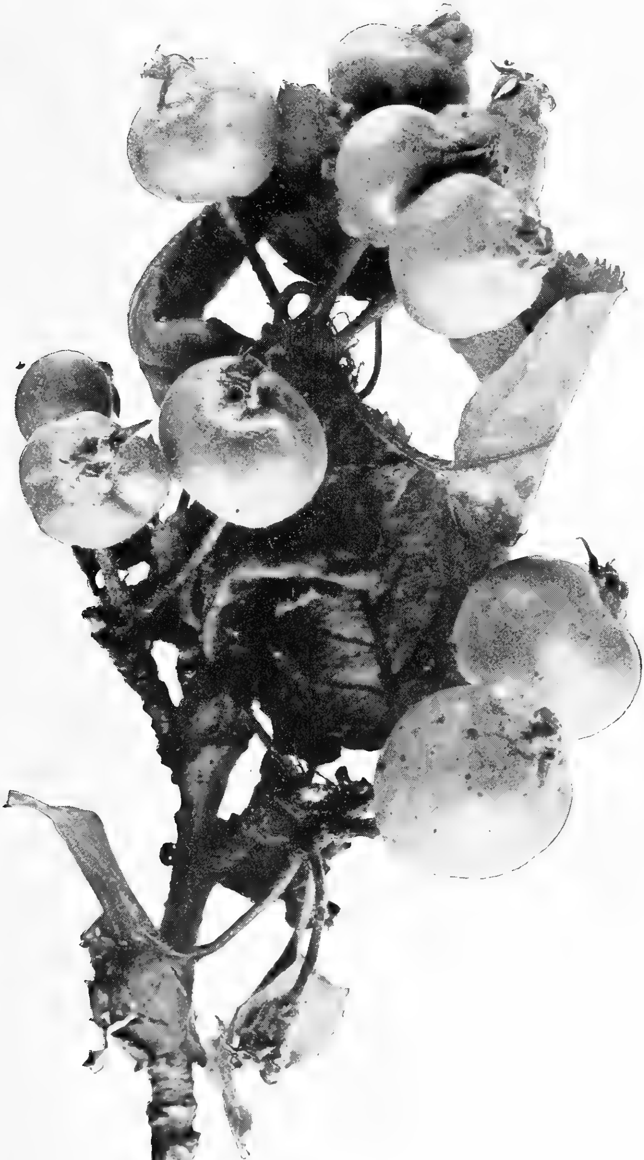
LEAVES OF TOMPKINS KING APPLES SEVERELY CURLED BY APHIS SORBI (MAY 27)

TIGHT LEAF ROLL CAUSED BY A SINGLE MOTHER AND A FEW YOUNG OF APHIS SORBI (MAY 25)



APPLE LEAF UNFOLDED TO SHOW A MASS OF APHIS SORBI

BALDWIN APPLES SEVERELY INJURED BY APHIS SORBI (JULY 26, 1916). NATURAL SIZE



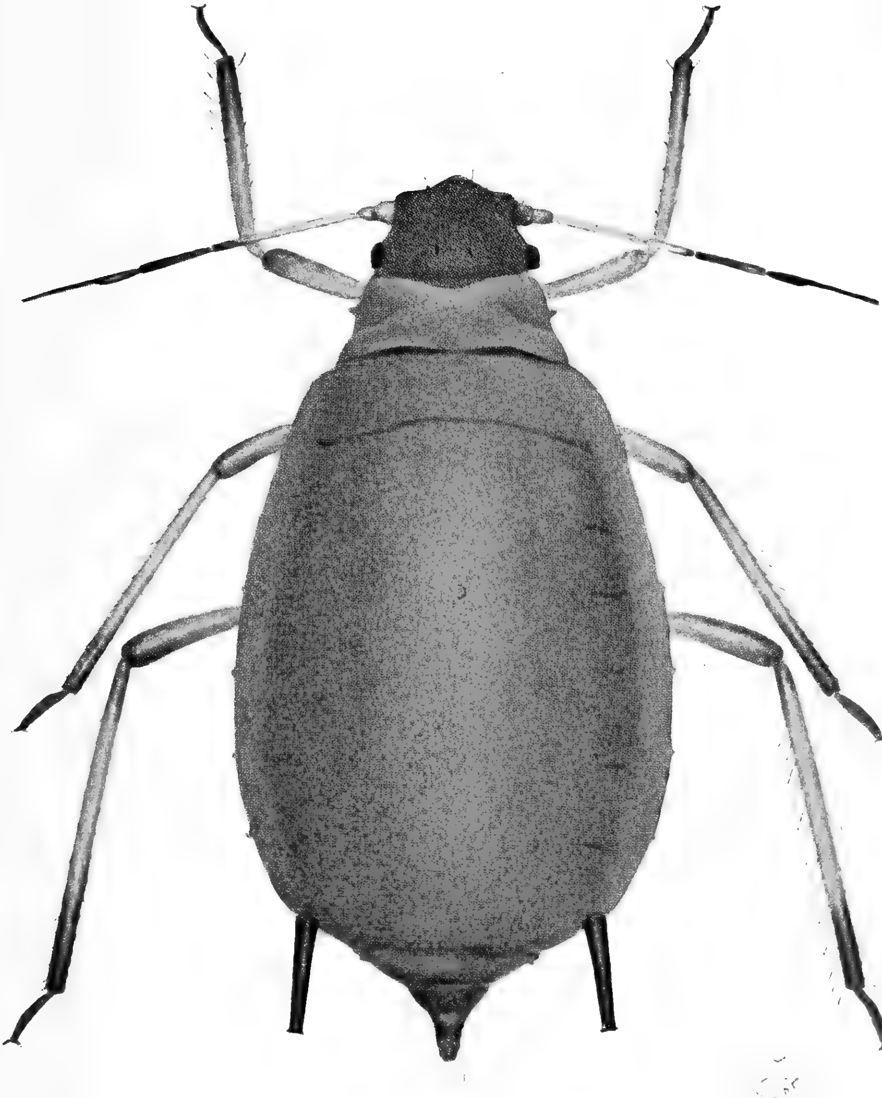
FALL PIPPIN APPLES SEVERELY INJURED BY APHIS SORBI (JULY 26, 1916). NATURAL SIZE

MAIDEN BLUSH APPLES SEVERELY INJURED BY APHIS SORBI (JULY 26, 1916). NATURAL SIZE

A B C

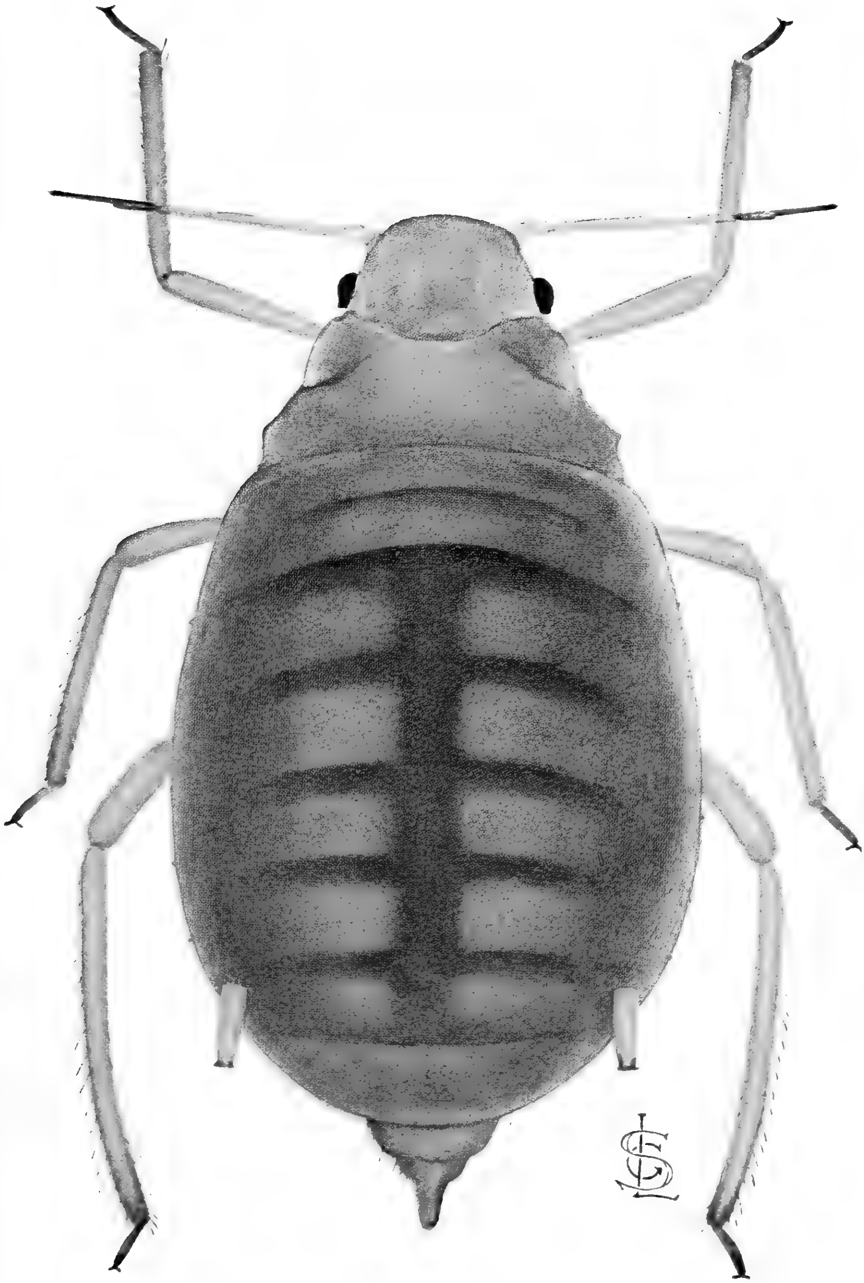
FIRST INSTARS OF STEM MOTHERS

A, Aphis pomi; B, Aphis sorbi; C, Aphis avenae. All drawn to same scale

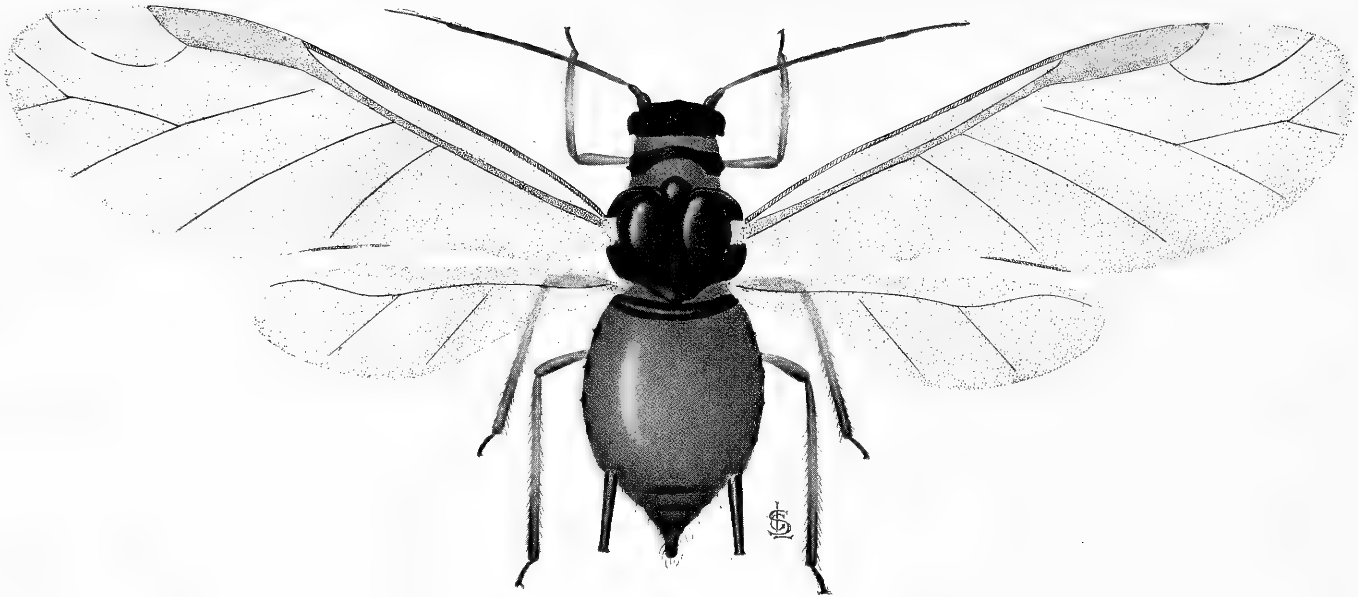


APHIS POMI, MATURE STEM MOTHER. × 60

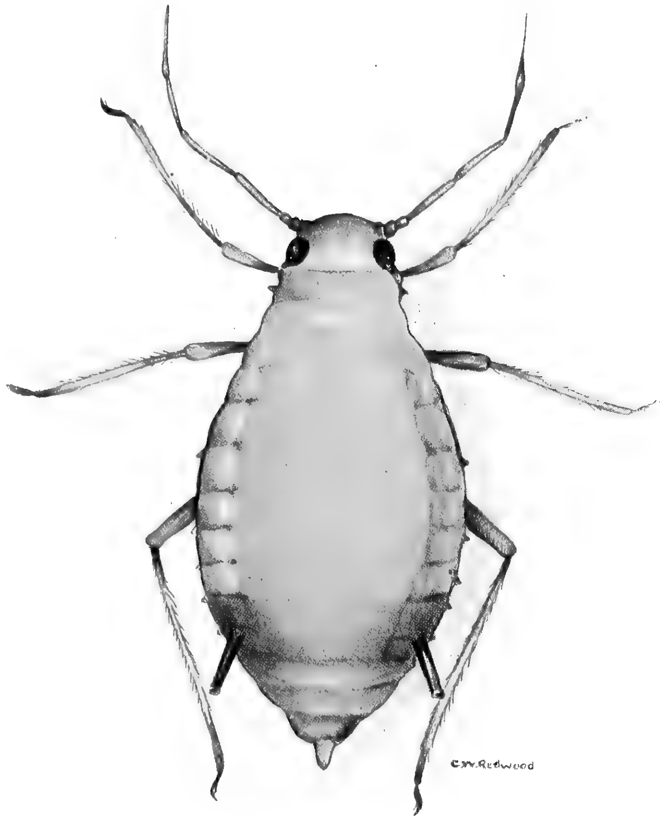
APHIS SORBI, MATURE STEM MOTHER. × 60



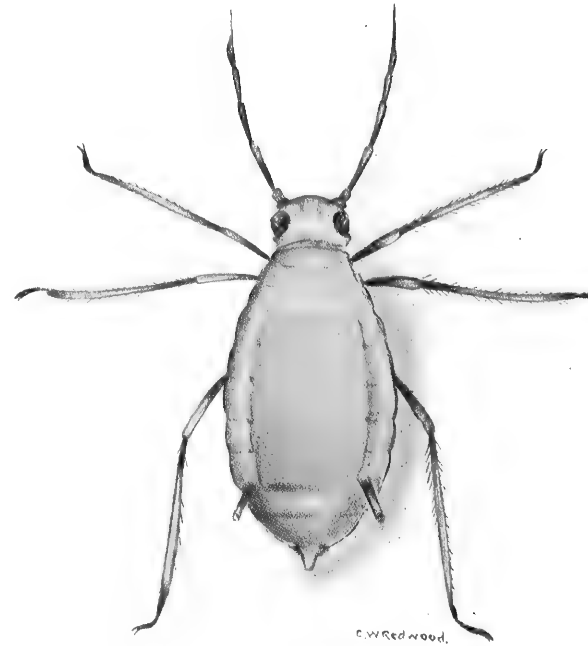
APHIS AVENAE, MATURE STEM MOTHER. × 60



APHIS POMI, WINGED VIVIPAROUS FEMALE, THIRD GENERATION



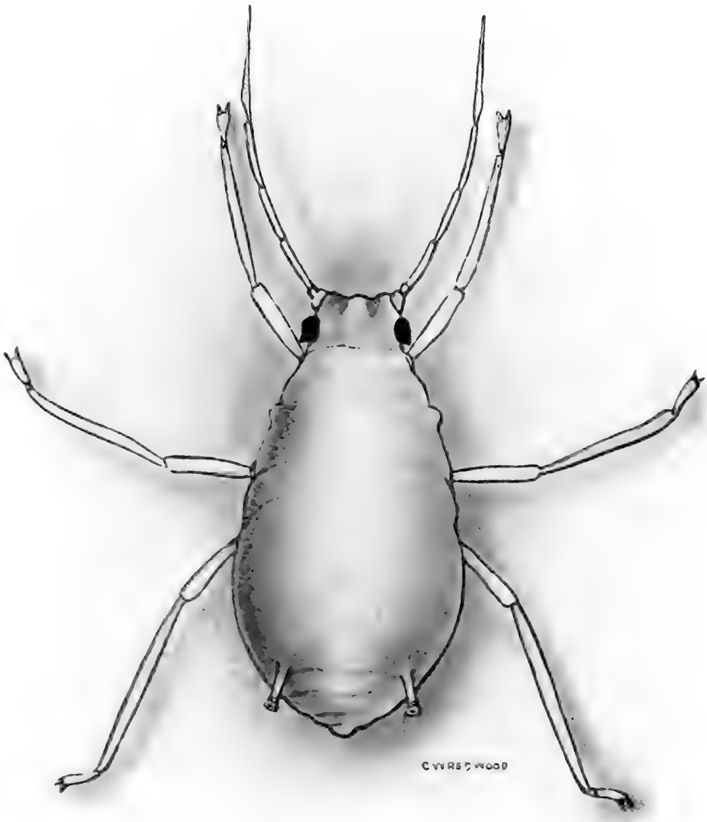
APHIS POMI, MATURE OVIPAROUS FEMALE



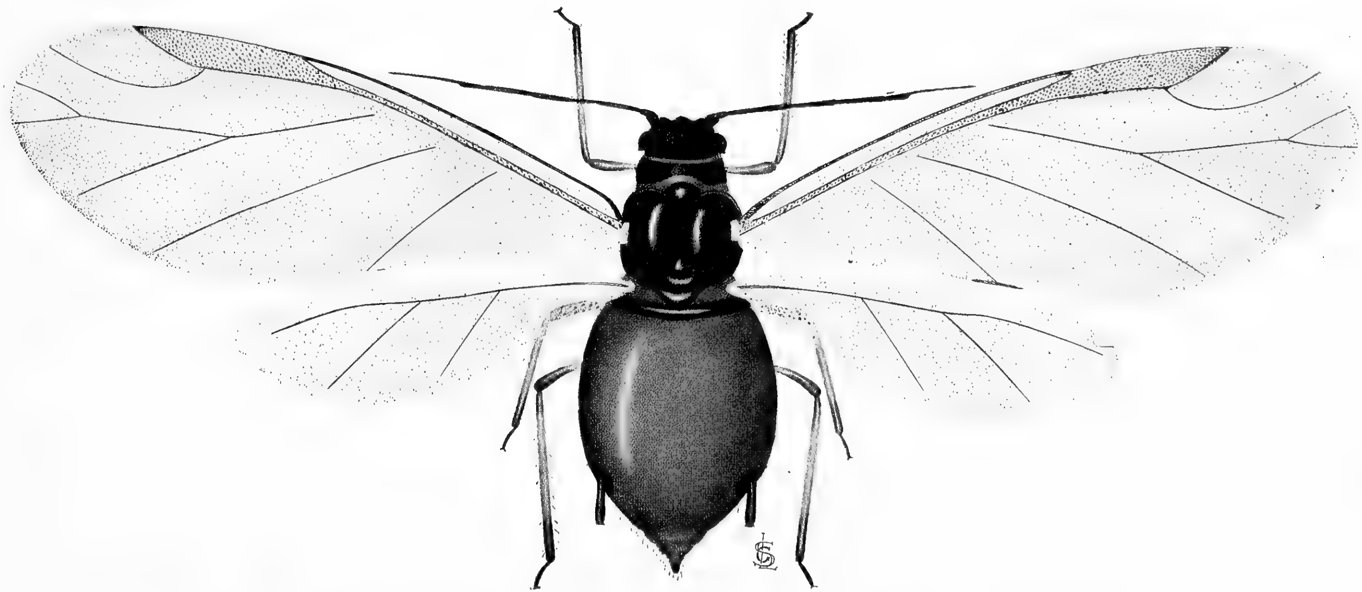
APHIS POMI, MATURE MALE

APHIS SORBI, SPRING MIGRANT TO NARROW-LEAVED PLANTAIN

APHIS SORBI, RETURN MIGRANT FROM PLANTAIN TO APPLE

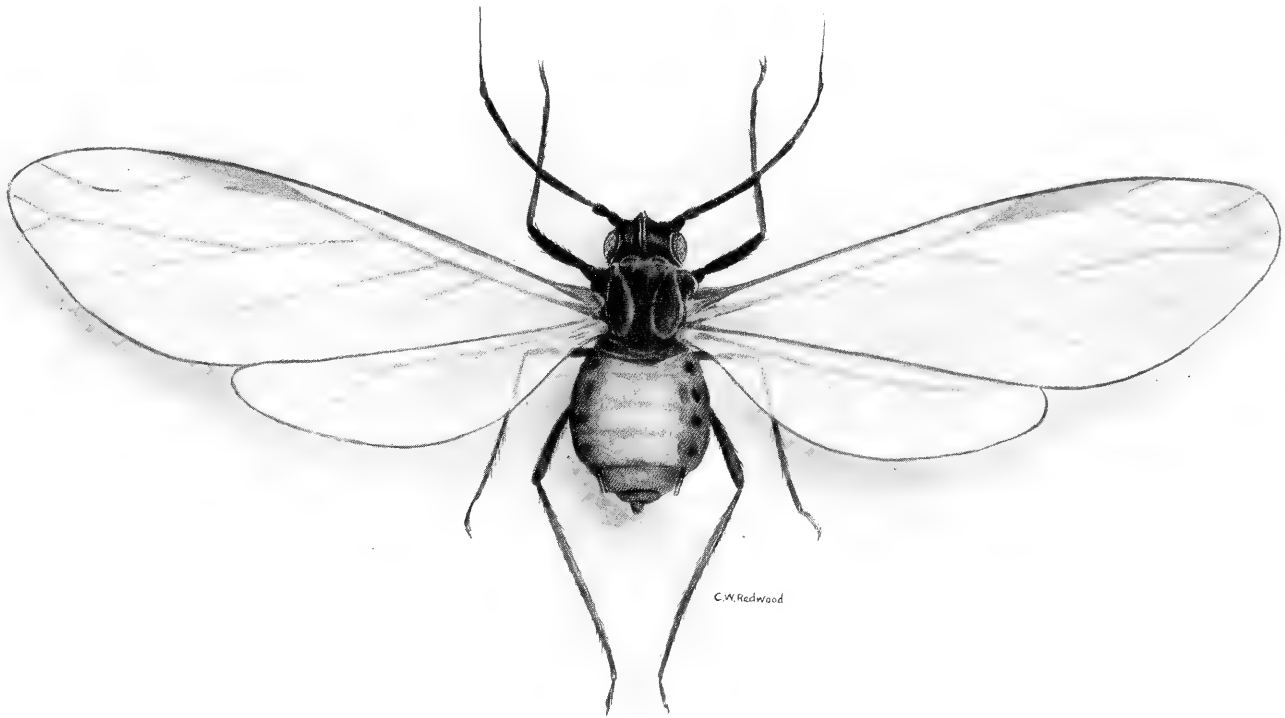


APHIS SORBI, MATURE OVIPAROUS FEMALE

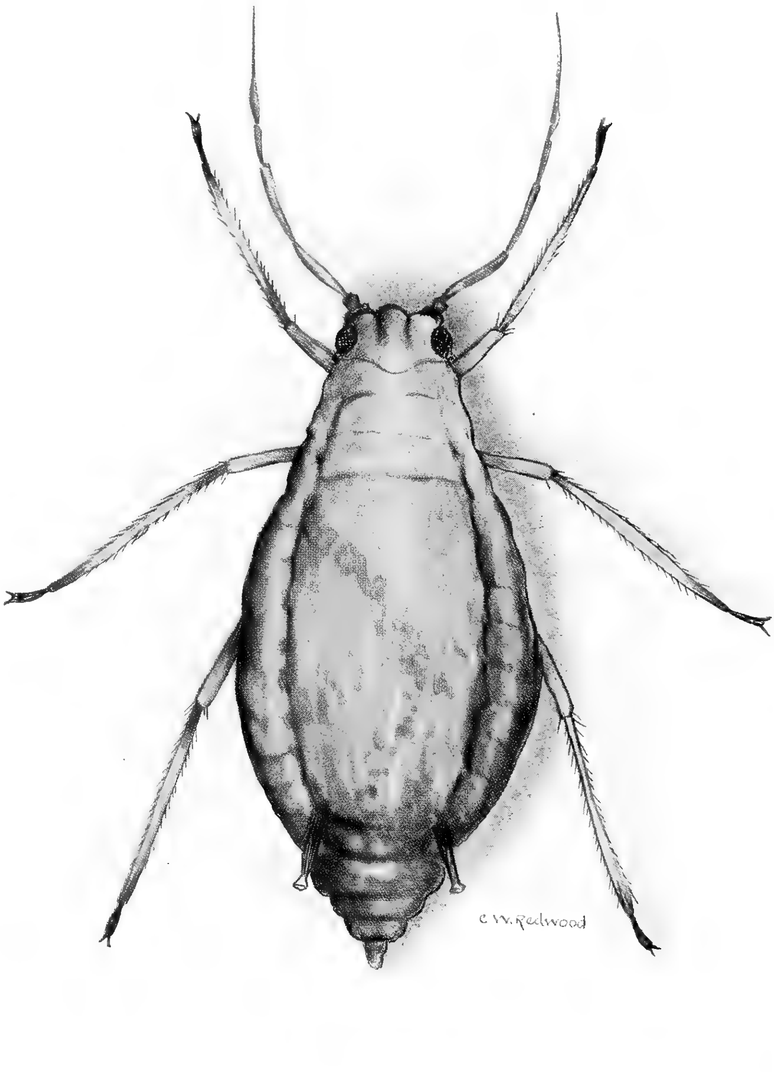


APHIS AVENAE, SPRING MIGRANT FROM APPLE TO GRAINS AND GRASSES

Plate XXVIII



APHIS AVENAE, FALL MIGRANT FROM GRAINS AND GRASSES TO APPLE



APHIS AVENAE, MATURE OVIPAROUS FEMALE

being that of Britton (1910) and more recently those of Brittain (1915 b) and Baker and Turner (1916 b).

Altho this plant louse has been present for some time over a large section of the United States, it did not assume the status of an important apple pest until late in the nineteenth century. This is readily understood when it is considered that this species, in order to thrive, must have near at hand an abundance of its summer host plants, the narrow-leaved and broad-leaved plantains (*Plantago lanceolata* L. and *P. major* L.). From the writer's rearing experiments and field observations, it may be concluded that the narrow-leaved plantain (*P. lanceolata*) is the preferred host plant; in fact it appears to be essential, at least at Ithaca, to the continued reproduction of the species during the summer. Breeding experiments on broad-leaved plantains were never successful for more than two or three generations, the line dying off, sometimes very quickly. This agrees with the results of Baker and Turner (1916 b), altho Ross (1915) and Brittain (1916) report very successful breeding experiments on *P. major*.

Introduction and spread of summer host plants

The two species of plantains *Plantago major* L. and *P. lanceolata* L. are importations from Europe. *P. major* appeared early, in all probability with the first permanent settlers in New England. Josselyn[4] records it as present in New England and following closely the habitats of the white settlers. So closely was it associated with the white man's coming that the Indians named it *Englishman's foot,* as tho it was produced by his treading. Bigelow[5] reports it as a common roadside weed in New England. Oakes[6] lists it as common about the houses and roadsides of Vermont. Since his time it has spread over the entire country. Its habitat is along beaten paths, by dusty roadsides, and in similar locations. In the northern sections of the United States and Canada there are two varieties, or perhaps good species, which possess thin leaves and occur in entirely different habitats. These are listed by Fernald[7] as *Plantago major* var. *intermedia,* which is found along salt

[4] Josselyn, John. New England's rarities discovered: in birds, beasts, fishes, serpents, and plants of that country, p. 1–114. 1672.

[5] Bigelow, Jacob. Florula Bostoniensis, p. 1–268. 1814.

[6] Oakes, Wm. Catalogue of Vermont plants. *In* History of Vermont, natural, civil, and statistical, by Zadock Thompson, part 1, p. 173–208. 1842.

[7] Fernald, Merritt L. Some recently introduced weeds. Massachusetts Hort. Soc. Trans. **1905**: 11–22. 1905.

marshes, and *P. major* var. *asiatica,* occurring along river banks and in moist situations thruout Canada and the northern United States.

The narrow-leaved plantain, *Plantago lanceolata,* is first recorded by Cutler[8] as not common in the meadows of New England. Bigelow[9] lists it as a common weed thruout the meadows of New England. Hitchcock[10] records it as prevalent in the meadows about Amherst, Massachusetts. Oakes[11] does not record it as present in Vermont, altho undoubtedly it must have reached southern Vermont at the date of his writing. The westward spread of *P. lanceolata* has been gradual and erratic. Hendrick[12] lists it from Onondaga County, New York, in 1834 and 1835. It is reported by Dewey[13] as being present in and about Rochester in 1841. Engelmann[14] does not record it as present in Illinois, tho only thirteen years later Lapham[15] reports it as one of the common plants there; evidently its introduction into Illinois was very widespread, due, of course, to the rapid opening up of the State. Winchell[16] observes that *P. major* is widespread in Michigan, whereas *P. lanceolata* is recorded from Ann Arbor only. Lapham[17] does not list *P. lanceolata* in his study of the flora of Wisconsin, and Upham[18] omits it from his list of the plants of Minnesota. Neither species is reported from central Colorado by Porter and Coulter[19], and Rydberg[20] states that both species are rare in the Rocky Mountain region. It is interesting to note that both species are first recorded from Oregon in 1896 as occurring on the Lander experimental farm, both undoubtedly having been introduced. Since that time

[8] Cutler, Manasseh. An account of some of the vegetable productions, naturally growing in this part of America, botanically arranged. Amer. Acad. Arts and Sci. Memoir **1**:396–493. 1785.

[9] See footnote no 5, page 721.

[10] Hitchock, Edward. Catalogue of plants, growing without cultivation. *In* Report on the geology, mineralogy, botany, and zoology of Massachusetts, p. 599–651. 1833.

[11] See footnote no. 6, page 721.

[12] Hendrick, J. L. A catalogue of plants found growing chiefly in the vicinity of Onondaga Academy, collected during the summer of 1834 and 5. Regents Univ. State of New York. Ann. rept. **1837**:182–188. 1837.

[13] Dewey, Chester. Catalogue of plants, and their time of flowering, in and about the city of Rochester, for the year 1841. Regents Univ. State of New York. Ann. rept. **55**:265–272. 1842.

[14] Engelmann, George. Catalogue of a collection of plants made in Illinois and Missouri, by Charles A. Geyer. Amer. journ. sci. and arts 1:**46**:94–104. 1844.

[15] Lapham, I. A. Catalogue of the plants of the State of Illinois. Illinois State Agr. Soc. Trans. **2**:492–550. 1857.

[16] Winchell, N. H. Catalogue of phaenogamous and acrogenous plants found growing wild in the lower peninsula of Michigan and the islands at the head of Lake Huron. Michigan Geol. Survey. Bien. rept. prog. **1**:245–330. 1861.

[17] Lapham, I. A. Plants of Wisconsin. Wisconsin State Agr. Soc. Trans. **2** (1852):375–419. 1853.

[18] Upham, Warren. Catalogue of the flora of Minnesota, including its phaenogamous and vascular cryptogamous plants, indigenous, naturalized, and adventive. Minnesota Geol. and Nat. Hist. Survey. Ann rept. **12** (1883)[6]:5–193. 1884.

[19] Porter, Thomas C., and Coulter, John M. Synopsis of the flora of Colorado. U. S. Geol. and Geog. Survey Terr. Misc. pub. 4:1–180. 1874.

[20] Rydberg, P. A. Flora of Colorado. Colorado Agr. Exp. Sta. Bul. 100:i–xxii, 1–448. 1906.

both species have spread to a considerable extent in the orchard sections of that and other Western States. P. A. Lehenbauer, Botanist of the University of Nevada, informs the writer that neither species is reported from Nevada, tho he thinks they may occur in some localities. It may be added that *Aphis sorbi* is not reported as being present in Nevada.

There is a remarkable parallelism between the introduction and spread of *Plantago lanceolata* and the spread and increasing destructiveness of *Aphis sorbi.* It has already been pointed out by the writer that this plant not only is the preferred, but seems to be the essential, summer host plant for this aphid. This statement is supported not only by experimental work but also by the study of the spread of the species. Had *Plantago major* been as favorable a summer host plant, the rosy aphis should have become abundant at an earlier date, as this plant was widely distributed thruout the country in advance of *Plantago lanceolata.* Had *Plantago major* var *asiatica,* a native thin-leaved variety found in Canada and the northern United States, been a favorable summer host plant, earlier outbreaks thruout the orchard areas of eastern Canada and the northeastern United States would have been expected. This is certainly not the case, as this aphis is first recorded as doing serious damage in the eastern United States and gradually working westward, northward, and southward in close relation with the spread of *Plantago lanceolata.* As has already been pointed out, neither species of plantain is abundant thruout the Rocky Mountain region. It is also well known that *Aphis sorbi* is not abundant nor seriously injurious in that region, except in certain restricted orchard sections where the narrow-leaved plantain has become well established. A very interesting situation is reported to the writer from British Columbia. In the coastal area *Aphis sorbi* has been abundant and destructive for a number of years, while in the interior valleys, where many of the larger orchards are found, this plant louse has appeared only in the last few years. *Plantago lanceolata* is reported by Macoun [21] as having been abundant in the coastal area since 1890, but it did not spread to the interior valleys until within the last few years. In consequence outbreaks of *Aphis sorbi* are now being reported from some of the larger orchard sections in the interior.

[21] Macoun, John. Catalogue of Canadian plants. Part II.—Gamopetalae, p. 193–394. Canada Geol and Nat. Hist. Survey. 1884.

Another interesting point in support of the above statement is the fact that *Plantago lanceolata* is primarily a plant of the meadows, thus providing ideal conditions for the development of *Aphis sorbi* in and about orchards. *Plantago major*, on the other hand, is a roadside weed, thick-leaved, sturdy, and well able to thrive under unfavorable conditions. Such a plant does not seem to be a favorable host for such a delicate insect as the summer forms of the rosy aphis.

DISTRIBUTION

Altho the species *Aphis sorbi* was first recorded in Illinois in 1854, it is still difficult, owing to the confused condition of the literature, to state its exact distribution. It has been definitely recorded from Delaware, New Jersey, New York, Connecticut, Maine, Ohio, Oregon, and Colorado, and from various sections of Canada particularly in the apple-growing sections of Ontario, Nova Scotia, Quebec, and British Columbia. In all probability this plant louse is widely distributed in the apple-growing sections of the United States and Canada, but it has been so confused with *Aphis pomi* and *Aphis avenae* that it is hopeless to try to untangle the various brief references.

NATURAL HISTORY

Aphis sorbi, like *Aphis pomi* and *Aphis avenae*, deposits its eggs on apple trees, and hibernation takes place, in the north at least, only in the egg stage. Hatching occurs early in the spring, about a week to ten days later than in the case of *Aphis avenae* and at about the same time as in *Aphis pomi*. For 1914 this was on April 26 and for 1915 on April 27. Close observations about Ithaca during the past three years clearly prove that comparatively few eggs of this species were deposited in this locality. As a result a very small number of the stem mothers were observed in the spring, yet, despite this fact, there was a severe infestation with serious loss of fruit in 1914, and there would also have been a similar condition in 1915 had there not been a timely application of adequate control measures.

Owing to the comparative rarity of the return migrants during the autumns of 1914 and 1915, very little work has been done on the egg stage of this species. The shy and wandering habits of the insects, combined with their scarcity, made futile any hopes for an adequate supply

of eggs. As a consequence no observations have been made on the failure of the eggs of this species to hatch due to the various factors which seem to play such a large part in the case of *Aphis pomi.*

The stem mother

The young, as soon as they hatch, actively seek out the opening buds of the apple, seeming to prefer the fruit buds. Under normal conditions close search has to be made for this species, as it usually occurs in very small numbers mingled among the abundant individuals of *Aphis pomi* and *A. avenae.* However, the whitish pulverulence, or powder, which covers its more or less dark purplish body readily serves as a distinguishing character. This pulverulent condition is especially marked after the second molt.

The stem mothers of this species differ considerably in their habits from those of the other two common species of apple aphids. As soon as the buds open, this species is most commonly found congregated about the opening flower buds; into these they penetrate, frequently attacking the flower stalks as the buds unfold. Some of the insects settle on the underside of the leaves, quickly causing them to curl.

The severe curling of the foliage caused by this species is in all probability the most characteristic feature of its work. A single stem mother located on the underside of a leaf near the midrib will cause the leaf to fold almost as tightly as the outer wrappings of a cigar (Plate XIV). As to the active agent which causes such a reaction on the part of the plant, scarcely anything is known. It requires the presence of only a few stem mothers to cause a severe curling of all the leaves surrounding an opening flower bud, and within such curls ideal protection is afforded to the rapidly developing plant lice. This work of curling the foliage so severely in the spring is due to this species alone; *Aphis pomi* causes only a partial folding, usually doing no more than bringing the tip and the base of the leaf into contact and never producing a close curl. Furthermore, *Aphis sorbi* is rarely found attacking the young and rapidly growing shoots, restricting itself to the foliage, the flower stalks, and the young fruit.

The stem mothers reach maturity at the time when the apple trees are coming into bloom. The blooming time varies from year to year, but in 1915 the first stem mothers became mature and began bringing forth young on May 10, just as the earliest blossoms were opening. In

1914 the earliest date on which stem mothers became mature was May 16, and this corresponded with the first unfolding of the blossoms.

The mature stem mothers are very inactive. They settle down and content themselves with pumping out the plant juices and producing young at a most phenomenal rate. When disturbed they quickly remove the proboscis from the plant tissues and seek out another spot in which to continue their operations.

Reproductive period

The stem mothers become mature in about two weeks after hatching; the length of time depends largely on weather conditions, tho under the most favorable circumstances nearly two weeks are required. The production of young usually begins in two or three days after the last molt, and continues without interruption for over a month. The stem mothers are remarkably hardy and their productive capacity is wonderful. As the warm, sunny days of spring come on, the plant louse seems to turn into a reproducing machine, and each morning the worker is filled with astonishment as he carefully removes and counts the overnight progeny, seemingly greater in bulk than that of the mother. This rate of production continues day after day, as may be seen by consulting Reproduction Chart II. In these experiments the average daily production thruout the productive period was 5.45 for four individuals. The greatest number produced in one day was 33, while the average length of the productive period was 33.5 days. The total production of young by the various individuals varied from 131 to 244, with an average of 184.

In the case of this species the period of reproduction extends from about May 10 to June 20 or later. As the eggs of this species hatch over a period of ten or more days, undoubtedly the last stem mothers to hatch are still producing during the last week of June. However, the maximum period of productive activity is during the last week of May and the first week of June, that is, while the young fruits are beginning to set and start active growth.

Description of stages

First instar (Plate XVIII).— Average length 0.6 mm.; average width 0.3 mm. (There is considerable variation in these measurements, dependent on the age of this instar.)

REPRODUCTION CHART II. APHIS SORBI

Reproductive capacity of stem mother, 1915

No.	May																				
	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31
108	1	..	5	2	1	1	0	2	0	1	6	4	7	2	7	7	4	4	6	5	11
109	2	4	3	2	1	2	1	2	1	1	1	10	6	2	11	0	8	8	5	1	13
110	..	3	6	3	5	1	5	3	4	1	5	10	6	8	5	5	9	1	11	4	7
111	..	1	5	4	3	3	2	3	2	3	3	7	3	3	7	4	5	0	5	1	6

No.	June																						Productive period (days)	Average daily production	Greatest number produced in one day	Total number of young	Date of death	Total length of life (days)
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20								
108	10	10	18	5	2	10	18	8	7	2	1	5	3	2	2	1	0	0	..	..	..	..	37	4.86	18	180	June 19	54
109	4	18	17	4	4	0	0	0	..	..	..	..	..	..	..	..	..	..	..	..	..	..	26	5.04	18	131	June 5	39
110	11	9	19	0	14	14	33	8	6	5	3	8	0	5	1	2	3	1	0	0	..	..	38	6.42	33	244	June 26	59
111	7	18	3	4	14	7	15	10	10	3	8	10	2	0	0	..	..	..	..	..	..	..	33	5.48	18	181	June 14	47
Averages...........																							33.5	5.45		184		49.7

Reproductive capacity of second generation, apterous female, 1915

No.	May			June															
	29	30	31	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
118	..	..	..	..	..	3	2	5	4	13	6	4	4	4	5	4	8	6	3
120	..	..	..	..	..	..	..	2	8	11	8	5	7	4	13	9	11	5	12
134	..	..	..	2	1	3	5	1	4	14	6	1	9	4	3	6	3	5	1
137	7	0	4	6	5	4	1	4	1	8	8	2	7	3	3	6	9	5	6
139	4	0	0	0	1	8	4	4	9	14	7	7	5	6	6	4	7	3	7

No.	June														July										Productive period (days)	Average daily production	Greatest number produced in one day	Total number of young	Date of death	Total length of life (days)
	17	18	19	20	21	22	23	24	25	26	27	28	29	30	1	2	3	4	5											
118	6	3	6	1	2	5	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	21	4.52	13	95	June 26	43
120	17	6	22	8	1	6	5	1	3	2	1	1	0	2	0	1	0	1	0	..	..	..	..	..	30	5.73	22	172	July 15	61
134	0	0	0	1	0	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	20	3.45	14	69	July 24	38
137	4	6	8	12	2	6	3	3	7	3	1	1	3	0	..	..	..	..	..	..	..	..	..	..	32	4.62	12	148	June 30	47
139	9	5	2	0	0	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	22	5.09	14	112	June 20	37
Averages																									25	4.68		119.2		45.2

REPRODUCTION CHART II. APHIS SORBI (*continued*)

Reproductive capacity of third generation, apterous female, 1915

No.	June																		July											Productive period (days)	Average daily production	Greatest number produced in one day	Total number of young	Date of death	Total length of life (days)
	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	1	2	3	4	5	6	7	8	9	10	11						
141			8	8	6	8	12	5	10	5	6	7	4	6	6	6	7	8	6	7	3	1	1	1	0					22	5.95	12	131	July 10	36
142		2	7	6	8	5	21	5	10	6	5	4	8	5	10	8	8	7	2	3	2	2	1	0	0					22	6.14	21	135	July 12	39
143					5	8	10	7	7	5	10	3	8	5	4	8	10	7	10	7	9	4	1	1						20	6.45	10	129	July 30	55
149					7	9	7	5	2	8	5	5	7	4	7	8	16	5	8	5	5	3	5	0	1	1	1	0	0	23	5.39	16	124	July 18	43
152	4	6	9	2	12	9	8	4	6	2	1	5	4	2	1	7	6	3	5	7	3	3	0	6	2	1	0	0		26	4.54	12	118	July 17	46
Averages																														22.6	5.69		127.4		43.8

Reproductive capacity of winged migrant (spring), 1917

No.	June				July																												Productive period (days)	Average daily production	Greatest number produced in one day	Total number of young	Date of death	Total length of life (days)
	27	28	29	30	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28						
305	11								14		2		1		0																		15	1.87	......	28	July 14	30
306	6								15		4		6		1			1			0		0										20	1.65	......	33	July 23	39
309	12								9		4		0		1			1			0												20	1.35	......	27	July 19	35
312	15								9		5		5		2			3			0		0										20	1.95	......	39	July 28	44
313	10								17		2		2		0			3			1		0		0		1		2			2	34	1.18	......	40	July 28	44
Averages																																	21.8	1.60		33.4	....	38.4

REPRODUCTION CHART II. APHIS SORBI (*continued*)

Reproductive capacity of second generation, apterous female on plantain, 1917

No.	July																									August								Productive period (days)	Average daily production	Greatest number produced in one day	Total number of young	Date of death	Total length of life (days)
	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	1	2	3	4	5	6	7	8						
317	7		5		7			10			7		13		8		11		9			9		3		3			1		1		1	34	2.79	......	95	Aug. 20	58
319			3		8			8			10		4		9		13		12			4												22	3.23	......	71	July 30	33
320			6		7			10			9		5		10		9		6			12		2		1								26	2.96	......	77	Aug. 4	40
321			6		6			9			8		10		6		10		7			11		3		3			2		1		0	31	2.61	......	82	Aug. 20	56
323			5		6			9			2		0		8		7		6			14		10		7			5					29	2.72	......	79	Aug. 6	42
Averages																																		28.4	2.87		80.8		45.8

Reproductive capacity of third generation, apterous female on plantain, 1917

No.	July											August																						Productive period (days)	Average daily production	Greatest number produced in one day	Total number of young	Date of death	Total length of life (days)
	21	22	23	24	25	26	27	28	29	30	31	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22						
326	3		5		7			14		11		17			6		3		7			4		0		5			1		0			29	2.86	......	83	Aug. 29	49
327	4		2		9			13		8		14			12		3		7			0												19	3.79	......	72	Aug. 11	33
328	2		4		6			8		8		5			12		6		5			8		5		4			2		4		0	31	2.55	......	79	Sept. 5	47
331			5		9			16		4		10			10		5		5			3		2		1			0		1		0	30	2.37	......	71	Sept. 8	61
334			4		11			13		8		10			7		6		5			6		4		1			5		0		0	28	2.86	......	80	Aug. 29	50
Averages																																		27.4	2.89		77		48

REPRODUCTION CHART II. APHIS SORBI (*continued*)

Reproductive capacity of fourth generation, apterous female on plantain, 1917

No.	August																															September											Productive period (days)	Average daily production	Greatest number produced in one day	Total number of young	Date of death	Total length of life (days)
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	1	2	3	4	5	6	7	8	9	10							
342	4			6		5		7			11		5		9			9		5		6			2		1		0														27	2.59		70	Sept. 1	42
343	2			6		4		5			6		6		5			11		7		7			7		0																25	2.64	......	66	Sept. 22	63
344	2			3		6		3			7		5		3			3		4		4			9		6		3			3		0									32	1.91	......	61	Sept. 3	44
349				2		5		5			8		2		8			5		5		6			7		3		4			1		0		0			1				36	1.72	......	62	Sept. 10	48
350				2		4		3			4		4		5			7		3		5			5		2		3			2		3		2			1		1	*a*	47	1.25	......	59	Sept. 29	67
																																Averages											33.4	2.02		63.6		52.8

a 1 on September 12, 15, and 19, respectively.

Reproductive capacity of fifth generation, apterous female on plantain, 1917

No.	August												September																														Productive period (days)	Average daily production	Greatest number produced in one day	Total number of young	Date of death	Total length of life (days)
	20	21	22	23	24	25	26	27	28	29	30	31	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	..	..	..	..						
359	3		3			15		5		4			4		7		2			3		1		0			0		1		0												29	1.65	......	48	Sept. 19	44
362	1		6			9		6		6			6		5		2			3		0		2			2		2		5			3		0		3	*b*				41	1.56	......	64	Oct. 1	55
364			3			9		6		5			14		4		3			1		0																					18	2.50	......	45	Sept. 12	36
366						4		4		5			10		6		0			3		3		0			6		3		4			2		2		5	*c*				40	1.50	......	60	Oct. 15	66
367						2		3		4			12		6		0			2		1		0			3		2		1			2		1		1	*d*				43	1.05	......	45	Oct. 21	72
																																				Averages							34.2	1.65		52.4		54.6

b 3 on September 29.
c 1 on September 29, October 1, and October 3, respectively.
d 4 on September 29, 1 on October 6.

REPRODUCTION CHART II. APHIS SORBI (*concluded*)

Reproductive capacity of sixth generation, apterous female on plantain, 1917

No.	Sept. 5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	Oct. 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15		Productive period (days)	Average daily production	Greatest number produced in one day	Total number of young	Date of death	Total length of life (days)
376	2	..	..	4	..	2	..	2	..	..	7	..	4	..	2	..	..	6	..	3	..	4	..	..	4	..	3	..	1	..	..	4	..	2	..	0	..	..	2	..	0	*e*	47	1.17	......	55	Nov. 5	75
377	..	..	..	4	..	2	..	2	..	..	5	..	3	..	4	..	..	5	..	2	..	2	..	..	6	..	3	..	3	..	..	2	..	1	..	1	..	..	1	..	2	*f*	52	1.00	......	52	Oct. 29	66
379	..	..	..	..	..	2	..	1	..	..	4	..	2	..	2	..	..	7	..	0	..	4	..	..	6	..	0	..	2	..	..	5	..	2	..	1	..	..	0	..	0	*g*	57	0.77	......	44	Nov. 16	81
380	..	..	..	..	..	4	..	1	..	..	3	..	0	..	3	..	..	3	..	2	..	5	..	..	2	..	4	..	4	..	..	1	..	0	..	0	..	..	0	..	2	*h*	42	0.90	......	38	Nov. 4	70
381	..	..	..	2	..	2	..	1	..	..	4	..	5	..	2	..	..	6	..	1	..	5	..	..	4	..	3	..	4	..	..	2	..	0	..	0	..	..	2	..	0	*i*	52	0.94	......	49	Nov. 5	72
Averages																																											50.0	0.96		47.6		72.8

e 3 on October 21.
f 3 on October 21, 1 on October 29.
g 3 on October 21, 1 on October 29, 2 on November 5.
h 3 on October 17, 1 on October 21.
i 5 on October 21, 1 on October 29.

Reproductive capacity of seventh generation, winged female on apple (fall migrant), 1917

No.	Oct. 6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	Nov. 1	2	3	4	5	Productive period (days)	Average daily production	Greatest number produced in one day	Total number of young	Date of death	Total length of life (days)
543	9	..	..	..	2	..	..	0	..	..	..	3	..	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	18	0.83	......	15	Oct. 21	34
544	9	..	..	..	1	..	..	0	..	..	..	0	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	7	1.43	......	10	Oct. 17	30
545	9	..	..	..	2	..	..	1	..	..	..	0	..	..	..	0	..	..	..	..	..	..	..	0	..	..	..	..	..	..	1	29	0.45	......	13	Nov. 16	60
546	12	..	..	..	2	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	10	1.50	......	15	Oct. 17	30
547	9	..	..	..	0	..	..	3	..	..	..	0	..	..	..	1	..	..	..	..	..	..	..	1	..	..	..	..	..	..	..	26	0.54	......	14	Nov. 5	51
Averages																																18	0.95		13.4		41

The general color is dark green, with a row of small black spots on each side of the median dorsal line; the antennae, the eyes, two large quadrate areas on the dorsal surface of the head, the legs, and the cornicles, are black. The sides of the body show a distinct whitish pulverulence, especially toward the end of the instar; the ventral surface is covered with a marked white pulverulence. The cornicles (fig. 111, B, page 684) are long and cylindrical, constricted before the apex, which is distinctly flanged. The antennae are 4-segmented, long, reaching about halfway between the end of the thorax and the base of the cornicles; the unguis is more than twice as long as the basal part of the segment (fig. 111, B, page 684).

Second instar.— The second instar does not differ in any respect from the first except as to size. The whitish pulverulence, however, is more pronounced.

Third instar.— Length 1.44–1.52 mm.; width 0.72 mm.

The coloration varies greatly, not only in different individuals but in the same individual, during this instar; in general the dorsal surface is yellowish green mottled with yellow; the sides are darker green, and completely covered with a fine white pulverulence; around the base of the cornicles and between them the color is reddish brown to red. The head is dark, with two tubercles on the hind margin. The antennae are 5-jointed, pale on the basal third, on the remainder dusky to black. The eyes are prominent and black. The cornicles are cylindrical, slightly flaring at their tips, brownish to black. There are pointed, black, lateral tubercles on the prothoracic segment and on all the abdominal segments except the last two; on the last two abdominal segments are black bands bearing a tubercle on each side of the median line. The cauda is scarcely visible, black. The legs are dusky to black. The ventral surface is covered with a beautiful white pulverulence.

Fourth instar.— Length 1.9 mm.; width 1.04 mm.

The general coloration is the same as for the preceding instar, but with a tinge of bluish in the greenish ground color. The entire body is covered with a beautiful white pulverulence. The antennae are 6-jointed. There are no other differences between this and the preceding instar.

Fifth instar, mature stem mother (Plate XX).— Length 2.25 mm.; width 1.44 mm.

The body is broadly pear-shaped, tending to globular in older specimens. The coloration varies greatly, not only in different individuals but also in the same individual during its life; in general the abdomen is yellowish green mingled with purplish brown, the sides being usually dark purplish brown; the head and the thorax are dark brown tending to purplish; around the cornicles and between them the color is often reddish; the legs are yellowish, with the femora, the distal ends of the tibiae, and the tarsi, fuscous to black. The entire body is covered with a fine white pulverulence. The head bears two short tubercles on the vertex. The eyes are black. The prothorax bears a pair of black dorsal tubercles as well as a lateral tubercle on each side. The remaining thoracic segment, and each of the first six abdominal segments, bear a pair of black lateral tubercles; the seventh and eighth abdominal segments, each have a transverse, dorsal, chitinous plate bearing two pointed tubercles, one on each side of the median line. The antennae are 6-jointed, fuscous at the base with the remainder black. The length and number of sensoria of the segments (fig. 112, c, page 685) are as follows: Segment III, 0.32 mm., sensoria 0; Segment IV, 0.24 mm., sensoria 0; Segment V, 0.22 mm., sensoria 1; Segment VI, 0.1 mm. + 0.22 mm., sensoria the usual group.

The second generation

In 1915 the first young were produced by the stem mothers on May 11 and reached maturity on May 26. In general the second generation required from fourteen to twenty days to reach maturity and begin to produce young.

One of the most characteristic features of this species is the congregation of the young about the mother. Each individual stem mother or group of mothers will have massed about it hundreds of young, so that the infested leaves may be so covered as to be actually more than one layer deep (Plate XIV). This gregarious habit soon causes the death of the infested leaves and the consequent migration of the aphids. However, when several stem mothers congregate on a single leaf, forced migration soon follows owing to the lack of available space. The young move actively and hurriedly, seemingly anxious to locate a suitable feeding ground. It is at this period that they are so frequently found congregated on the forming fruits or attacking the new and succulent unfolding foliage.

The majority of this generation are wingless females; at least this has been the case in the writer's rearing experiments. In the field considerable numbers of winged forms developed, about 25 per cent so far as the writer could judge. These undoubtedly migrated to the summer food plant, tho no direct observations were made in the field. In cage experiments the winged forms readily reproduced on plantain as well as on apple.

Reproductive capacity

The second generation begins active reproduction during the last few days of May and reaches its maximum about the middle of June. The length of the individual productive period varies from 20 to 32 days, the average being 25 days. As the stem mothers continue reproducing until the latter part of June, the productive period of the second generation extends from the last few days of May until about the middle of July, the maximum reproduction occurring about the middle of June or slightly later. The average daily production (4.68) is lower than that of the stem mother, and the total production of each individual (average 119.2) is much less.

Description of stages

First instar.— Length 0.8 mm.; width 0.44 mm.; cornicles 0.08 mm. long. The young, when just born, are light cream-color thruout and are very active. The antennae and the legs are long, giving the young insect a sprawling appearance. The eyes are at first reddish but soon turn black. The distal ends of the tibiae and the tarsi become black shortly after the insect hatches. The entire body soon becomes covered with a delicate white pulverulence. The length of this instar is 2+ days.

Second instar.— Length 1 mm.; width 0.5 mm.; cornicles 0.12 mm. long. The general color and markings are similar to those of the first instar; there is a faint tinge of red in the yellowish ground coloring, otherwise no difference can be observed. The length of this instar is 2+ days.

Third instar.— Length 1.2 mm.; width 0.8 mm.; cornicles 0.2 mm. long. The general color is yellowish, with the sides of the abdomen around the bases and between the cornicles reddish; the head is somewhat dusky. The entire body is covered with a fine white pulverulence. The antennae are 6-jointed, with the basal half yellowish and the remainder black.

The cornicles are cylindrical, black, slightly flaring at the tips. The legs are yellowish, with the distal ends of the tibiae and the tarsi black. Black lateral tubercles are present on the prothorax and on the first six abdominal segments; the seventh and eighth segments each bear a pair of small black tubercles, one on each side of the median line. The length of this instar is 4+ days.

Fourth instar.— Length 1.6 mm.; width 0.9 mm.; cornicles 0.28 mm. long.

The general color is yellowish, with pink or reddish on the sides and around and between the cornicles. The whole body is covered with a delicate white pulverulence. The antennae are 6-jointed, fuscous. The legs are yellowish, except for the distal ends of the tibiae and the tarsi, which are fuscous to black. Small black lateral tubercles are present on the prothorax and on the first six abdominal segments; on the seventh and on the eighth abdominal segment is a pair of small dorsal tubercles, one on each side of the median line. Thele ngth of this instar is 4+ days.

Fifth instar.— Mature apterous viviparous female.—Length 1.84 mm.; width 1.04 mm.; cornicles 0.36–0.4 mm. long.

The recently molted female is dark purplish brown to olivaceous in color, with considerable spotting of light greenish on the dorsal part of the abdomen; the central part of the head and the anterior margin of the prothorax are yellowish; around the base of the cornicles and on a broad band between them the color is reddish. The entire body is covered with a beautiful white pulverulence. The cornicles are cylindrical, slightly tapering, flaring at their tips; the color is reddish yellow on the basal part, with the distal half black. The antennae are 6-jointed; the basal half is lemon-yellow, the distal half fuscous to black. The eyes are black and tuberculate. The legs are yellowish, with the distal ends of the femora, the tibiae, and the tarsi fuscous to black. Lateral tubercles are present on the prothorax and on all the abdominal segments except the seventh and the eighth; the last-named bear small dorsal tubercles, one on each side of the median line.

The apterous females vary greatly in coloration. The commoner form is the one just described. All gradations, to the form described as follows, may be discovered by a close examination of a wide series of individuals: general color yellowish, the sides faintly tinged with pink or reddish; around the cornicles, and a band between, dark red; basal half of

antenna yellow, remainder black; legs yellow, the distal ends of the tibiae, and the tarsi, black; cornicles yellow, tips black.

Winged viviparous female.— Length 1.44 mm.; width 0.8 mm.; cornicles 0.24 mm. long; wing expanse 5–6 mm.

The head is black, with the tubercles on the vertex prominent. The eyes are red to almost black, and tuberculate. The antennae are 6-jointed; the color is black except for the two basal segments, which are fuscous. The thorax is shining black. The base of the femora is banded with yellowish, the remainder is black; the tibiae are yellowish brown, with the distal ends black; the tarsi are black. The abdomen is yellowish brown at the sides and the base, with the dorsal part fuscous to black; around and between the cornicles the color is reddish yellow. The cornicles are cylindrical, gradually tapering, somewhat flared at the tips, black. The cauda is short and fuscous. Lateral tubercles are present on the prothorax and on all the abdominal segments except the seventh and the eighth, each of which bears two dorsal tubercles, one on each side of the median line.

The third generation

In 1915 the descendants of the second generation — that is, the third generation — began reaching maturity on June 12. In the writer's large rearing cage, where the seedling trees had become very crowded with the plant lice, the majority of the insects, in fact nearly all, acquired wings and migrated to their summer food plant. However, many did not acquire wings and these began producing another generation on the apple. The writer's observations in the field during the past season (1917) led to the conclusion that the majority of the lice of this generation did not acquire wings but settled down and produced a fourth generation on the apple. When such conditions occur there results a serious infestation, with consequent damage to foliage and fruit.

In 1915 the wingless females of the third generation began producing young on June 12, and the productive period extended well into July. In the case of five normal individuals the average producing period was 22.6 days, while the daily production averaged 5.69. The productive capacity averaged 127.4, which is considerably lower than that of the stem mothers but somewhat higher than that of the second generation.

The habits and activities of the third generation do not differ from

those of the second. The lice congregate in immense numbers on the underside of the foliage, causing severe curling; they also attack the setting and developing fruit, producing their characteristic injuries which are described later. At Ithaca in 1915, the majority of this generation acquired wings and migrated to their summer host plants.

When the last skin is shed the winged adults are very tender and inactive. They remain secreted in the curled leaves for several days, generally two or three, before venturing on their migratory flight. They then become very active and nervous, running about or moving their wings up and down in anticipation of their flight. What factors influence the production of winged or wingless forms in this generation can only be conjectured. In cage experiments where in some cases crowding became excessive, practically all of this generation acquired wings; whereas under similar conditions in other cages many of the insects did not acquire wings and produced a fourth generation on the apple. Many theories have been advanced, based entirely on observation, as to the influence which climatic factors, such as heat, cold, or moisture, may have; excessive crowding also has been used very generally in explaining the early production of winged forms. Unfortunately, thru lack of equipment no experiments could be undertaken by the writer to determine the influence of any of the factors involved. The importance and significance of the development of the winged migrants in any particular generation are very great, not only to the biologist, but also, and more particularly, to the orchardist. This is pointed out in more detail in the discussion of the summer migration of this species.

Description of stages

The early instars of the third generation are practically identical with those of the second generation, both in size and in color markings. It will therefore be sufficient to describe only the last two instars of this generation, restricting the description to the winged forms; the wingless forms are practically identical with those of the preceding generation and require no special description.

Fourth instar, winged female.— Length 1.8–2 mm.; width 0.9–1 mm.; cornicles 0.26–0.28 mm. long.

The general color after the molt is a bright pink, which gradually changes to a rusty reddish over the entire abdomen, the wing pads shading to

a reddish yellow; the head, the distal half of the antennae, the cornicles, and the distal ends of tibiae and tarsi, are black; the femora and the proximal parts of the tibiae are yellow. The entire body is covered with a rather dense white pulverulence. The lateral and caudal tubercles are present and appear as small dark spots.

Fifth instar, mature winged female (*spring migrant*) (Plate XXIV).—Length 1.44–2 mm.; width (wing expanse) 5–6 mm.; cornicles 0.32–0.38 mm. long.

The head is black above, with the median ocellus protruding and appearing as a tubercle. The antennae, the dorsal part of the thorax, a large quadrate area on the dorsum of the abdomen, the cornicles, the distal half of the femora, the distal ends of the tibiae, and the tarsi, are black; the proximal ends of the femora, and the tibiae except the tips, are yellowish brown; on each lateral margin of the abdomen in front of the cornicles are three rounded black areas; in front of the large quadrate black spot on the abdomen there are narrow transverse black lines in some specimens, but these are frequently lacking; around the base of the cornicles the color is black, and this is often fused with the black quadrate areas; the remainder of the body is of a yellowish brown color. The wings are hyaline, with the veins thin and the stigma dusky. The eyes are tuberculate and black; on the vertex between them is a pair of small tubercles. The prothorax has a prominent tubercle on each side. The abdomen has small but distinct lateral tubercles and prominent dorsal tubercles on the last two segments. The cauda is conical, short, setose, and provided with two or three pairs of long curving hairs. The cornicles are cylindrical, faintly imbricated, curved, and distinctly flanged on the distal end (fig. 115, c, page 706).

The antennae (fig. 114, c, page 705) are 6-jointed. Segments I and II are imbricated on their inner margins and armed with a few short, sharp spines; Segment III has numerous sensoria, varying from 50 to 60, the imbrications showing faintly; Segment IV is similar to Segment III, but bears only about half the number of sensoria, varying from 20 to 30; Segment V has only from 4 to 10 sensoria, and the imbrications are more distinct; Segment VI is strongly imbricated, and the unguis is short and bears the usual group of sensoria at its distal end. The length of the segments is as follows: Segment III, 0.6–0.7 mm.; Segment IV, 0.44 mm.; Segment V, 0.28 mm.; Segment VI, 0.12 + 0.56 mm.

The fourth generation

Altho the majority of the third generation under experimental observation acquired wings, a goodly number were wingless and were easily induced to continue reproducing on the apple. Their young constitute the fourth generation on apple.

The habits and activities of this generation do not differ in any respect from those of the third. The leaves, especially those about the fruit clusters, become crowded by the lice, which swarm also on the developing fruits. In 1915 they began reaching maturity about June 25, and from that date to the middle of July large numbers of winged forms were present on the apple trees. All those under experimental conditions acquired wings, and in the field, so far as could be learned by constant observation, all of this generation became winged and constituted the main spring migration of the years 1915 and 1917.

As the nymphal stages are practically identical with those of the second and third generations, it is not necessary to repeat detailed descriptions. The adult corresponds so closely to that of the third generation that the description of the winged female of that generation will serve in this case.

The migratory forms

At Ithaca the migratory forms of *Aphis sorbi* may consist of the winged females of either the second, the third, or the fourth generation (counting the stem mothers as the first generation). At Vienna, Georgia, Baker and Turner (1916 b) found that the migratory forms may appear in every generation from the third to the eighth on the apple. The writer did not succeed in rearing more than four generations on the apple, tho repeated attempts were made. However, from field observations and from notes in the files of the Department of Entomology at Cornell University, it would appear that in some years there are undoubtedly more than four generations in certain sections of New York State. As yet there are no definite data to prove or disprove such a belief. Brittain (1915 b) finds that in Nova Scotia the migratory forms are the winged adults of the third generation. He reports, however, that in individual rearing experiments, in which the number of plant lice to each seedling was very small, he succeeded in rearing a total of seven generations on the apple. In some experiments no migrants were produced. Brittain does not state

the number of generations of the latter that were reared. In the spring of 1915 the main migration at Ithaca consisted of the adults of the fourth generation, tho a large proportion of the third generation also migrated to the summer food plants. In 1916 there was only a slight infestation about Ithaca and practically all of the third generation consisted of the winged migratory forms.

The factors which influence the early or late production of migratory forms have not been suggested by any worker. The necessity of investigating the influence of climatic factors is urgent. As has already been pointed out, this is a very interesting problem to the biologist, and to the fruit grower it is one of paramount importance. In 1915 there was a serious outbreak of *Aphis sorbi* in New York State and the amount of damage done was very great. This was largely due to the fact that a comparatively small proportion of the third generation produced migrants. As a result the enormous numbers of the third generation produced young at a very rapid rate, resulting in the most serious infestations. The writer saw an orchard which, about the early part of June, showed only the usual marginal infestation in the lower branches. In this case the third generation (young) was appearing in large numbers and it was thought most of them would become migrants. For some unknown reason scarcely any of these produced winged forms, and as a result the trees became so infested that scarcely a leaf or a fruit could be found that was not crowded with the lice. When this generation (the fourth) became nearly mature there was not sufficient nourishment for them and they migrated in thousands to the branches and trunks, while the ground under the trees was literally swarming with them. As this orchard was well cultivated, the majority of the aphids died, tho thousands reached maturity and migrated to adjacent fields where the narrow-leaved plantain was growing in abundance. In this one small orchard the owner estimated his loss at from $800 to $1000. If the factors involved in the early or the late production of the winged migrants could be determined, this would be a long step in solving some problems in insect control.

There is another important point which cannot be overlooked at this time. Ross (1915) reports that he succeeded in rearing this species thruout the season on apple in Ontario, Canada, tho he presents no definite data. If this condition should become prevalent, there would be an instance

of a species that normally migrates to a summer host plant gradually acquiring the ability to reproduce continuously on its primary host. The production of a maximum of eight broods on apple at Vienna, Georgia, and the rearing experiments of Brittain (1915 b), would lend support to Ross's experimental work.

Another point of considerable importance is whether, during the summer, winged or wingless forms on plantain can migrate to apple and produce generations thereon. Brittain (1915 b) succeeded in one case in making such a transfer, using the progeny of the fourth generation on plantain. These matured and produced young which developed into the plantain forms. The writer has not succeeded in making such transfers, but in 1915 an infestation of this aphid was found on a Northern Spy on August 5. At that time only a few leaves were infested, and developing young, both winged and wingless, were present. This infestation became severe by August 25, but shortly thereafter all the aphids transformed to winged individuals and left the tree. Where this infestation came from is a mystery, as no lice had been present early in the season, and moreover the tree had been thoroly sprayed at least twice with Black-leaf-40 tobacco extract and soap. Neighboring apple trees had not a single plant louse present, nor did any lice appear later in the season. All about these trees there was a very abundant growth of narrow-leaved plantain, but no lice could be found on them at the time of the first appearance of the infestation on the Northern Spy tree.

Habits of the migratory forms

The spring migratory forms are very lively, and in the rearing cages they fly actively about, particularly in the bright sunshine. In the cages inclosed with cheesecloth they congregated in large numbers on the sunniest side and seemed very strongly attracted to the light. They would walk actively about, opening and shutting their wings, and seemed to be tiptoeing gently across the cloth in a very nervous manner. Gradually they discovered the narrow-leaved plantains in the cages (Plate VIII) and settled on them. Altho several broad-leaved plantains were also present they left these alone. Usually within from two to three days these winged forms began producing young, and then they became much more quiescent while their broods of young congregated closely about them.

The summer host plants

For many years the summer host plants have been searched for in vain. It remained for Ross (1915) to first record his successful transfer experiments to the broad- and narrow-leaved plantains (*Plantago major* and *P. lanceolata*). He states also that this species was reared thruout the summer on apple where crowding was prevented.

The experiments of the writer prove that at Ithaca the narrow-leaved plantain, or rib grass (*P. lanceolata*), is the preferred summer host plant and also in all probability the necessary summer host plant. In numerous experiments this species of lice could be reared on *P. major* for only two or three generations, when the line would die out, due to unknown causes; whereas under similar conditions the insects would continue to thrive on *P. lanceolata.* The results of these experiments are in accord with the work of Baker and Turner (1916 b), tho not with that of Ross (1915 and 1916) and of Brittain (1915 b). The more important reasons for believing that *P. lanceolata* is the necessary host plant, and that only here and there has this species of lice acquired the ability to use *P. major*, have already been pointed out in the historical discussion. Of course it is very probable that owing to the adaptability of *Aphis sorbi* and the abundance of *Plantago major*, the insect may eventually use either summer host plant without any marked preference as shown at present.

Ross's statement that this aphid can maintain itself thruout the season on apple is very important. Unfortunately, his statement is not supported either by the work of Baker and Turner (1916 b) or by that of the writer, tho Brittain (1915 b and 1916) records experiments in which he carried the species thru the summer on apple in Nova Scotia. This important phase in the life cycle of this species needs more investigation, for should the species become able to thrive on apple thruout the season it might become a pest of the first magnitude.

The summer forms

The spring migrants, after settling down on the plantain, begin producing living young within two or three days. All of their immediate descendants are wingless viviparous females. The young congregate about their mothers and are commonly found on the underside of the lower leaves, at the base of young, tender leaves, or on the developing

flower stalks. The young grow very rapidly, and under favorable conditions become mature within from ten to fifteen days. Thruout the summer months breeding is continuous and generation follows generation with considerable rapidity. During the summer of 1916 at least six generations matured on the plantain. By the first week in August of that year the fourth generation was mature and ready to produce young. Then there came very dry, hot weather, which continued until well into September. During this time the lice were rather inactive, failed to grow rapidly, and died off in large numbers. Only on the lower leaves and at the base of the flower and leaf stalks did the aphids survive, and it was almost impossible to follow closely the number of generations.

During the summer of 1917 a more detailed study was made of the reproductive capacity of the summer generations on plantain. Starting with the spring migrants from the apple, continuous rearing experiments were conducted thruout the season. In 1916 the rearing experiments were conducted in large cages, in each of which several narrow-leaved plantains were growing under natural conditions (Plate IX). In this way enormous numbers of the young were obtained, considerable crowding occurred, and, as later noted, winged forms appeared in several generations. In 1917 the rearing work was all done on young narrow- and broad-leaved plantains growing in small pots in an outdoor insectary. By this method close observation could be made on the individual reproductive capacity, and, tho many hundreds of individuals were reared, only one winged form appeared on the plantain. This occurred in the third generation on plantain, counting the winged as the first.

In Reproduction Chart II and figure 120 is presented a rather interesting study of longevity and reproductive capacity of the spring and fall migrants, as well as the true summer forms, on their preferred host plant (*Plantago lanceolata*). It will be noted at once that the spring migrant shows a shorter longevity and a remarkable reduction in reproductive capacity as compared with the spring forms on the apple. The succeeding wingless generations are more productive than the winged migrants, the productive period is much longer, and the longevity is greatly increased; as compared with the forms on the apple, the longevity on the average is greater and the productive period is longer, whereas the reproductive

capacity is greatly lessened. In the case of the summer forms on plantain, no attempt was made to determine the daily reproductive capacity, the rearing cages being examined only as recorded in the chart. However, it will be observed that the daily average, which is very low as compared with the forms on apple, is fairly well distributed over a long reproductive period. This is not the case with the spring and fall winged migrants.

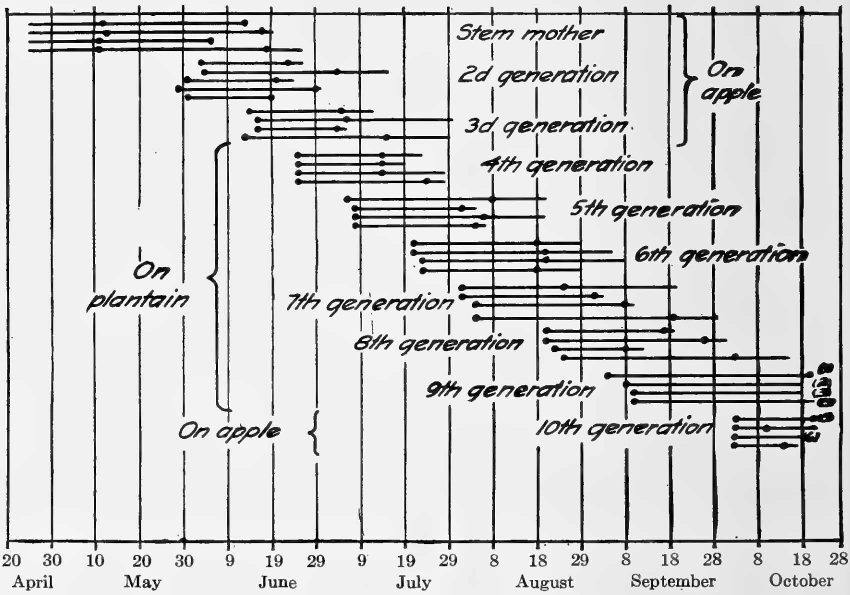


FIG. 120. GENERATIONS OF APHIS SORBI

The part of the line between the round dots represents the productive period; the remainder of the line represents the period of life after production ceased. The fourth generation all migrated to the plantain, and the tenth returned to the apple

(1) Died November 5; (2) died October 29; (3) ceased reproducing November 5, died November 16; (4) died November 4; (5) died October 21; (6) ceased reproducing November 5, died November 16

In these cases the reproductive period is reduced, whereas a marked reproductive activity occurs within the first few days after maturity is reached and the new host plant is occupied. The spring migrant gave an average daily production of 5.4 for five individuals during the first two days, followed by a daily production of only 1.4 during the next nine days. The fall migrant gave an average daily production of 3.2 for five individuals during the first three days, followed by only 0.34 during the next seven days, when reproductive activity practically ceased.

The reproductive activities of the spring and the fall migrants are undoubtedly due to the same factors, and are in marked contrast to those of the summer and spring forms. With the latter the rate of reproduction usually is low at first, gradually reaches its maximum, and then as gradually declines. The reproductive activities of the migrants can be explained, in all probability, in the following manner: They do not leave their host plants until a few days after reaching maturity, so that the reproductive organs are extremely active on reaching the new host plant. In order to avoid destruction by many agencies, such as climatic conditions, predatory enemies, or the like, it would seem essential that the greatest possible deposition of young should occur as soon as possible after the new host plant is found. So much of the vitality of these forms has been used in the production of wings and in the search for the new host plant, that a high reproductive capacity would seem physiologically impossible.

The summer generations consist very largely of wingless viviparous females. In 1916 winged forms appeared in the third, the fourth, and possibly the fifth generation, counting the descendants of the spring migrants as the first generation on plantain. In the third and fourth generations winged forms appeared in considerable numbers; the writer made no attempt, however, to determine the relative proportions of winged and wingless forms. This is in rather marked contrast to the results of Baker and Turner (1916 b), who record having observed but six winged forms thruout a summer's rearing work.[22] The winged forms developing in the large rearing cages were very active and flew about with great ease. Unfortunately the writer was unable to do much work with these forms, tho they reproduced normally and appeared well able to distribute the species during the summer. Whether these forms can return to the apple and breed there was not determined; the probability of such a condition has already been discussed (page 741).

Baker and Turner (1916 b) conclude that the summer winged forms are produced in such relatively small numbers that they are of no particular importance in the life history of the species. The writer cannot accept such a conclusion founded upon a single season's rearing work, particularly as different results were obtained at Ithaca. Furthermore, the large

[22] In the writer's rearing experiments of 1917, results similar to those of Baker and Turner were obtained. However, the writer does not consider such results as normal.

number of natural enemies which this aphid encounters on the plantain seems to necessitate a high productive capacity, which the species possesses, and also ability to spread to more distant host plants.

Habits of the summer forms

The summer forms on the plantain are much more active and agile than those occurring on the apple. Their legs are relatively longer when compared to the length of the body, and they can run with great rapidity. If an infested leaf or flower stalk is jarred or moved, the aphids at once remove their beaks and scurry rapidly for cover or drop to the ground. On the ground they hasten away and can travel considerable distances. In several rearing cages the aphids became so abundant that they caused the death of large plants. In such cases they climbed about the inside of the cage in immense numbers, endeavoring to find any possible exit. When the cages were opened they ran out very rapidly, and if they escaped their natural enemies it was not long before another plant was found. Undoubtedly this is the common way in which the species spreads from plantain to plantain during the summer.

Description of stages

Summer wingless viviparous female, adult.— Length 1.4–1.6 mm.; width 0.8 mm.; cornicles 0.4 mm. long.

The general color is light lemon yellow, usually with a faint reddish tinge on the dorsum of the metathoracic segment, and reddish yellow to reddish around and between the cornicles; in older specimens the color may become almost brown; the distal parts of the antennae, and the cornicles, the eyes, and the tarsi, are black. The antennae (fig. 114, D, page 705) are 6-segmented, slender, long, reaching beyond the tips of the cornicles. The segments are imbricated, and lack sensoria except an apical one on Segment V and the usual group at the distal end of the basal part of Segment VI. The length of the segments is as follows: Segment III, 0.4 mm.; Segment IV, 0.32 mm.; Segment V, 0.24 mm.; Segment VI, 0.12 + 0.36 mm. The head has a faint median tubercle; the dorsal tubercles are absent; the abdomen and the thorax lack the lateral and dorsal tubercles so prominent in the forms on apple. The cornicles are cylindrical, slender, slightly curved, and distinctly flanged (fig. 115, D,

page 706). The legs are long and slender, giving the wingless summer forms a slender and active appearance.

The above description is based largely on the adult wingless females of the first, second, and third generations on plantain, counting the descendants of winged migrants as the first generation. Tho there is considerable variation in size, and frequently in color markings, of the wingless females of each generation, yet these are not of sufficient importance to warrant special description.

Summer winged viviparous female.— This form appeared in considerable numbers in some of the writer's large rearing cages, which is in marked contrast to the results of Baker and Turner (1916 b). Descriptions of the fourth and the fifth (adult) instar follow.

Fourth instar.— The general color is bright red, except for the legs, the cornicles, the antennae, the head, and the wing pads; the head, the legs, the cornicles, and the basal half of the antennae are yellow; the apical half of the antennae, and the eyes, are black; the basal part of the wing pads is yellow, the tips brown to black; the cornicles are slightly dusky at their tips.

Fifth instar, adult.— Length 1.6 mm.; wing expanse 5 mm.

The winged summer female is almost identical to the spring migrant in color characters. The quadrate black area on the dorsum of the abdomen may be lacking in some cases, while in many others it is not so large as in the spring migrant. Otherwise there are no distinguishing characteristics.

Autumn forms

Late in the autumn there appear special winged forms which return to the apple. These are known as the autumn, or fall, migrants. They consist of winged viviparous females and winged males. They begin to appear in the region of Ithaca late in September, the winged females developing first. There is no general migration in the true sense of that term, as these winged forms continue to return to the apple thruout the latter part of September and the whole of October, reaching their maximum, however, about the middle of the latter month. Stragglers also appear in November. The males begin appearing somewhat later and continue migrating to the apple well into November.

Both the winged males and the winged females are active, capable of flying very considerable distances and of walking or running with considerable agility. In the rearing cages they would fly actively about, being strongly attracted to the sunny side, or would walk over the fine wire mesh or cheesecloth. When liberated they flew away with a vigorous, direct flight.

The winged female

The females on reaching the apple usually seek out the underside of the leaves. Here they secure nourishment and deposit their young — the wingless oviparous females. They do not produce large numbers of young, nor do they deposit them in any one place, but seem to prefer to migrate from leaf to leaf depositing but a few young at a time.

The early instars of this form are identical with those of the spring migrant in practically every detail, and therefore it seems unnecessary to repeat the details here.

The mature winged female, fall migrant (Plate XXV).— Length 1.7–2 mm.; wing expanse 6 mm.

The autumn migrant is somewhat larger and more robust than the spring migrant. In color markings it does not vary to any extent, and it is only necessary to refer the reader to the description of the winged female of the third generation on apple. These winged forms, however, are frequently darker than the spring forms, appearing almost black, and agreeing very closely with the description given by Fitch (1855 a).

The antennae are 6-jointed and black. The third segment bears about 60 sensoria, the fourth about 30, the fifth from 6 to 12, and the sixth the usual group. The length of the segments is as follows: Segment III, 0.6–0.72 mm.; Segment IV, 0.4–0.5 mm.; Segment V, 0.25–0.32 mm.; Segment VI, 0.12–0.15 mm. + 0.6–0.7 mm. The head lacks the dorsal tubercles present in the spring migrant; very small lateral tubercles are present on the prothorax and on the abdominal segments; the last two abdominal segments are without dorsal tubercles. The cornicles are cylindrical, slightly curved, and distinctly flanged at their tips (fig. 115, E, page 706).

The male

The males are not so numerous as the females and usually appear later in the season. They are not so heavy-bodied and are more active.

In general structural details and color markings they do not differ from the female fall migrants, and no further description is needed.

The males on reaching the apple seek out the descendants of the female fall migrants and mate with them if they are mature. A single male mates indiscriminately with as many of the oviparous females as he can find.

The oviparous female

The immediate descendants of the female autumn migrants are known as the oviparous females. They are rather inactive, are smaller than the ordinary apterous summer forms, and are wingless. They are found on the underside of the apple leaves, but the writer has never found them causing a curling of the foliage similar to that caused by the spring forms. This form requires from twenty to thirty days to reach maturity, the nymphal stages varying greatly in length owing to the changing temperature conditions.

The mature oviparous female (Plate XXVI) is from 1.2 to 1.5 mm. in length. The general color is lemon yellow, with a faint greenish tinge near the margins of the body; around and between the cornicles is a rusty-red reticulated area, which is very characteristic; the head is grayish and the eyes are black. The cornicles are cylindrical and are distinctly flanged at their distal ends. The cauda is short and conical. The antennae are long. Sensoria are lacking, except a distal one on Segment V and the usual group at the base of the terminal filament of Segment VI (fig. 118, B, page 715). The length of the segments is as follows: Segment III, 0.16–0.2 mm.; Segment IV, 0.12–0.16 mm.; Segment V, 0.1–1.2 mm.; Segment VI, 0.32–0.34 mm. Lateral and dorsal tubercles are not present on the abdominal segment. Numerous sensoria are present on the hind tibiae (fig. 119, C, page 716).

Oviposition.— The mature oviparous females migrate to the smaller twigs and branches. There mating usually takes place, and the eggs are deposited around the base of buds, under small pieces of bark, or in any sheltered position. The writer has not been able to determine the number of eggs laid by many females, but in the few experiments conducted from four to six eggs were laid. This agrees with the results of Baker and Turner (1916 b), who record an average egg production of 6.3 for each female.

The egg is oval in form, and is slightly flattened on the side next the bark. The length is from 0.48 to 0.56 mm. The color is identical with that of the egg of *Aphis pomi.*

THE APPLE-BUD APHIS, OR OAT APHIS

(*Aphis avenae* Fabricius)

The apple-bud aphis has been present in orchards in the eastern United States since the early part of the past century. It has been confused constantly with the two preceding species, *Aphis pomi* De G. and *A. sorbi* Kalt., and in many cases it is difficult if not impossible to determine to which species a writer is referring. It is not purposed in this article to present a detailed historical account of this species, inasmuch as this plant louse is a more serious pest of its summer host plants than of apple. However, it may be well to summarize briefly the synonymy of the species as it occurs in literature. This, according to the writer's views, is as follows:

1794 *Aphis avenae* Fabricius, Ent. Syst. **4** : 214.
1851 *Aphis mali* Fitch, Cat. Ins. Cab. Nat. Hist., p. 65.
1855 *Aphis mali* (in part) Fitch, Trans. N. Y. Agr. Soc. **14** : 753.
1886 *Aphis annuæ* Oestlund, Geol. and Nat. Hist. Surv. Minn., Ann. Rept. **14** : 43.
1887 *Aphis annuæ* Oestlund, Geol. and Nat. Hist. Survey Minn., Bul. 4 : 66.
1902 *Aphis fitchii* Sanderson, Del. Agr. Exp. Sta., Ann. Rept. **13** : 137.
1904 *Siphocoryne avenæ* Pergande, U. S. Div. Ent., Bul. 44 : 5.
1917 *Aphis prunifoliæ* Baker, Science (n. s.) **46** : 410–411.

NATURAL HISTORY

The bionomics of this plant louse have been studied by a number of writers. The following account deals only with its life history and habits in relation to the apple, its primary host plant.

The eggs of *Aphis avenae*, like those of the two species already discussed, are laid in the autumn on apple, and at Ithaca hibernation takes place in this stage tho the writer has found the species hibernating as wingless viviparous females about the base of its summer food plants. Whether it can succeed in living thru northern winters and continuing its activities in the spring has not been accurately determined.

The eggs begin hatching in the spring from a week to ten days earlier than those of the green apple aphis or the rosy apple aphis. In the past three years the first eggs hatched on April 19 (1916), April 17 (1917),

and April 15 (1918). Hatching continues over a considerable period, usually about ten days if the weather is favorable. The stem mothers become mature during the last few days of April and the first week of May.

In some years this plant louse is extremely abundant and may be found in great swarms on the opening apple buds. Since the stem mothers hatch at the time of the swelling of these buds, the lice may be found congregated at the very tips seeking entrance even before the tips show green. As the buds unfold, the lice feed indiscriminately on the tender foliage but do not cause any marked curling of the leaves. Altho the lice were extremely abundant in 1915 they did scarcely any damage. Undoubtedly they reduced the vitality of the foliage to some extent, but not enough to be noticeable as compared with the injury caused by *Aphis pomi* and *A. sorbi.*

The stem mother

In the species *Aphis avenae* the stem mothers reach maturity in about two weeks after hatching from the eggs. They feed almost exclusively on the opening foliage but do not cause any curling. They never attack the tender twigs, and have never been observed feeding on the water sprouts as is so common with the green apple aphis. The stem mothers become mature early in May. Altho a large number were reared in 1915, only a few were successfully carried thru the productive period. Deposition of young usually begins within from twenty-four to thirty-six hours after the last molt. In the individuals carried thru a normal life, the productive period was 30 days, the total production of young averaged 75, and the average daily production was 2.58. The total length of life was 44 days.

Description of stages

First instar (Plate XVIII).— The young nymph is dark green in color, with slightly lighter green down the middle of the dorsum; the head bears two black quadrangular areas on the dorsal surface, separated along the middle by a dark green line; the antennae, the legs, and the cornicles are almost black. The antennae are short, reaching to about the end of the thorax (fig. 111, c, page 684). The cornicles are very short, forming scarcely more than prominent disks (fig. 111, c). These last two characters readily separate this nymph from those of the other two species.

Second instar.— The color of the second instar is yellowish green, with the characteristic bright green diamond-shaped areas beginning to show on the dorsal surface of the abdomen; these, however, do not yet form a marked continuous line as appears in the later instars; the head is dark green; the legs and the cornicles are brown to almost black. The cornicles are still very short.

Third instar.— The third instar differs little from the second in color markings. The bright green diamond-shaped areas on the dorsum of the abdomen now form a continuous line, distinctly differentiating this species from the other two.

Fourth instar.— This instar is practically identical with the mature stem mother and does not require a separate description.

Mature stem mother (Plate XXI).— Length 2–2.15 mm.; width 1.2–1.3 mm.

The general color is yellowish green, the sides darker green; there is a broad median dorsal green stripe; at each segmental suture this stripe broadens out laterally, giving a somewhat diamond-shaped appearance to the green area of each segment; the distal ends of the antennae and the tibiae, the tips of the cornicles, and the tarsi, are dusky to black; around the base of the cornicles and between them there is frequently a reddish yellow area; the head is concolorous with the body; the eyes are black. The cornicles are cylindrical, slightly constricted at base and apex, with flaring tips (fig. 113, C, page 702). The antennae (fig. 112, B, page 685) are 5-jointed. The length of the antennal segments is as follows: Segment III, 0.32 mm.; Segment IV, 0.09 mm.; Segment V, 0.24 mm.

The second generation

The young nymphs of the second generation feed almost exclusively on the foliage; rarely have they been found on the developing fruit. At Ithaca the majority of this generation acquire wings and migrate to the summer host plants. A small proportion are wingless viviparous females and continue to produce young on the apple.

Description of stages

First instar.— The young nymph is yellowish green in color, with the mid-dorsal green stripe plainly visible; the tips of the antennae, the

distal ends of the tibiae, and the tarsi, are dusky; the cornicles are yellowish green, dusky to black at their tips. The cornicles are similar in shape to those of the first instar of the preceding generation.

Later instars.— The remaining instars are similar in all essential markings to the first and require no special description.

Mature viviparous female.— The general color of the mature female is light yellowish green, with a distinct mid-dorsal green stripe as in the stem mothers; the distal half of the antennae is dusky; the eyes are black; the basal half of the cornicles is yellowish green, the tips are dusky. The cornicles are cylindrical, slightly constricted at base and tip, the distal ends flaring. On the sides of the anterior abdominal segments a whitish pulverulence is often present.

The third generation

Normally there are comparatively few individuals of the third generation. All of them become winged and migrate to their summer host plants. The habits and characteristics of this generation are similar to the preceding and need no further discussion.

Description of stages

The nymphal stages differ in no essential from those of the preceding wingless generation. The developing wing pads readily distinguish the forms that are to acquire wings, but their color markings are essentially the same.

Winged viviparous female, spring migrant (Plate XXVII).— The winged female measures from 1.6 to 2 mm. long. The general color is dark green; the head, the antennae, the pronotum, and the thoracic lobes are dark olive-brown to black; the pronotum is margined in front and behind with yellowish green to dark green; on each side of the abdomen are three distinct black spots; at the base of the abdomen is a prominent transverse black stripe; the cornicles are brown to black, with a dark, almost black, area around the base; the legs are yellowish green except the tips of the femora and the tibiae, and the tarsi, which are dusky to black. The cornicles are cylindrical, constricted at the base and before the tips, which are flared somewhat irregularly (fig. 115, B, page 706). The antennae are shorter than the body and bear many characteristic sensoria

(fig. 114, B, page 705). The length of the antennal segments and the number of sensoria are as follows: Segment III, 0.3 mm., sensoria 8–10; Segment IV, 0.19 mm., sensoria 6–8; Segment V, 0.16 mm., sensoria 1; Segment VI, 0.1 + 0.35 mm., sensoria the usual group.

Summer life history

At Ithaca only three generations are normally produced on the apple. The winged migrants have practically all left for their summer host plants early in June, a few stragglers being found up to the end of that month. These summer host plants consist of a large number of grasses and cultivated grains; a full list is given by Davis.[23]

During the summer a large number of wingless and winged generations are produced. Late in the autumn, with the approach of cold weather, a winged migrating form appears, and this returns to the apple. At Ithaca these fall migrants begin to appear on apple and hawthorn about the last week in September. From that time to about the last week in October they continue to appear in increasing numbers, often in swarms. Their maximum flights probably occur about the last week in October. At that time they alight in great numbers on almost any object. They seem to be partial to white objects, and on examining white clothing hung out to dry it is very common to find on it great numbers of these lice.

The fall migrant

The fall migrant of *Aphis avenae* is more active than that of *A. sorbi*, and normally is found in much greater abundance. It continues to appear later in the season and settles in great numbers on apple and hawthorn species. The first migrants are all winged viviparous females, and as soon as they reach their food plants they settle on the underside of the leaves and feed. The males begin to appear about a week to ten days after the first females. Deposition of young begins usually within a day or two, and small colonies are soon found settling down close around the winged forms. Several such colonies can be readily found on a single leaf. As the season advances these colonies become more and more abundant.

[23] Davis, J. J. The oat aphis. U. S. Dept. Agr. Bul. 112:1–16. 1914.

An interesting feature of this situation is the great number of the young viviparous females that undoubtedly perish thru the falling of the leaves. On a hawthorn near the Cornell University campus, great numbers of migrants had settled in the fall of 1914. The oviparous females began oviposition on October 20. They probably reached their maximum numbers on the foliage about October 28, on which day there was a severe frost. By the evening of the 29th practically all the leaves had fallen, destroying thousands of the still immature oviparous females. Similar occurrences took place on neighboring apple trees, tho the falling of the leaves was not so marked. As a consequence comparatively few eggs were laid. This undoubtedly happens every year, particularly when there are early frosts followed by high winds.

Description of fall migrants

Winged viviparous female (Plate XXVIII).— The winged viviparous female is from 1.6 to 2 mm. long. The head, the pronotum, and the thoracic lobes are black, the last-named shining; the pronotum may be margined in front and behind with a narrow band of dark green, but these bands do not show clearly in many specimens; the antennae, the eyes, the distal lobes of femora and tibiae, and the tarsi, are black; the abdomen is green, with from three to four black spots on each side in front of the cornicles and a narrow black band at the base of the abdomen; caudad of the cornicles are a dark area on each side and one or two narrow dusky to black bands across the tip of the abdomen; the cauda is brownish or greenish brown; the anal plate is black; the legs, except as noted above, are yellowish green; the cornicles are brown to pale greenish brown. The cornicles are cylindrical, constricted somewhat at the base and before the apex, which is flared somewhat irregularly (fig. 115, F, page 706). The length of the antennal segments and the number of sensoria are as follows: Segment III, 0.32 mm., sensoria 12–16; Segment IV, 0.16 mm., sensoria 4–6; Segment V, 0.18 mm., sensoria 2–4; Segment VI, 0.8 + 0.46 mm., sensoria the usual group.

Winged male.— The winged male is from 1 to 1.5 mm. long. The general color markings are similar to those of the female, except that the abdomen is usually yellowish brown marked with considerable black in front of and between the cornicles; the antennae are black and about as long as the body; the cornicles are dark brown to black, and are similar in shape

to those of the winged female. The length of the antennal segments and the number of sensoria are as follows: Segment III, 0.24 mm., sensoria 14; Segment IV, 0.12 mm., sensoria 3; Segment V, 0.12 mm., sensoria 2; Segment VI, 0.8 + 0.35 mm., sensoria the usual group.

Oviparous female (Plate XXIX).— The oviparous female is from 1 to 1.3 mm. long. It is distinctly elongate-oval in outline. The general color is yellowish green, shading more or less to brownish green or in some cases to almost green; the antennae and the legs are somewhat brownish; the cornicles are short, brown to almost black; frequently there is an orange-colored or reddish yellow area around the base of the cornicles, but this may be absent in older specimens. The cornicles are cylindrical, constricted before the apex, which is markedly flared (fig. 117, B, page 714). The hind tibiae are somewhat enlarged and flattened, and bear from 29 to 32 sensoria (fig. 119, B, page 716). The cauda is distinct, tapering, bordered with three pairs of hairs. The length of the antennal segments (fig. 118, C, page 715) and the number of sensoria are as follows: Segment III, 0.18 mm., sensoria 0; Segment IV, 0.094 mm., sensoria 1; Segment V, 0.053 + 0.22 mm., sensoria the usual group.

The egg is oval in form, and is slightly flattened on the side next the bark. Its length is from 0.48 to 0.56 mm. In color it is identical with the egg of *Aphis pomi*.

EFFECTS OF ATTACKS OF PLANT LICE ON THE APPLE TREE AND ITS FRUIT

THE GREEN APPLE APHIS

The work of the species *Aphis pomi* is very characteristic and is easily distinguished from that of the other two species, *A. sorbi* and *A. avenae*. As soon as the apple buds begin to open, the lice congregate on the tips of the leaves and soon penetrate deep into the unfolding buds, inserting their beaks and sucking out the juices. They particularly attack the leaves and the flower stalks, and as soon as the tender shoots (Plate VII), especially the water shoots, form, they crowd in dense masses on these, frequently killing them outright. In these dense crowds of lice on the water shoots *Aphis avenae* also may be present, at least early in May, but *A. sorbi* is not present.

Aphis pomi is also a leaf-attacking form, and is generally found on the under surface of the leaf crowded about the midrib and the lateral veins.

When abundant the lice cause the leaves to curl, but not so markedly as does *Aphis sorbi.* The leaves never form a close, tight curl, as is so common with the latter species, but the curl is more open, the tip of the leaf rarely doing more than touching the base. Later in the summer, usually in late July and August when there is sometimes a severe outbreak of *Aphis pomi,* the curling of the foliage may be more marked (Plate X). This is particularly true as the lice congregate on the rapidly growing twigs, stunting them and causing all the foliage to curl badly and in many cases to turn black and die. In young orchards serious damage may be done by the dwarfing and stunting of the rapidly growing shoots.

As the fruit begins to set, it may be attacked by countless swarms of these green lice, which congregate about the calyx end, on the stalk, and around the base, of the apple. The action of these numerous pumps at work sucking out the juices of the apples causes them to become elongated, puckered, and distorted, with many characteristic creases on the surface (Plates X–XII). Such badly injured fruits may drop in great numbers in June, considerably reducing the expected crop; or they may remain on the trees and become hard and knotty, growing to a slight extent and usually forming clusters — the so-called "cluster fruits" (Plate XII). The apple crop has been seriously injured in this way in many sections in the past few years.

Where this plant louse is abundant it greatly reduces the vitality of the trees, prevents the formation of fruit buds, distorts and deforms the foliage, often kills many of the succulent shoots, and causes knotty and gnarled apples. Recent experiments have shown that it also seems to be an active agent in the transmission of fire blight, one of the worst diseases in nurseries and in apple and pear orchards.

THE ROSY APPLE APHIS

The rosy apple aphis (*Aphis sorbi*) hatches during the same period as the green apple aphis. It first attacks the opening buds, appearing to be particularly attracted to the flower buds (Plate XIII). In these the stem mothers congregate, and their progeny soon swarm over the developing leaves, the opening flowers, and the flower stalks. When the lice are abundant they may prevent the flowers from opening properly, and cause the flower stalks to weaken and oftentimes to bend to one side. The

leaves surrounding the cluster are severely curled, distorted, and usually blackened by the growth of a sooty fungus in the honeydew. When the infestation is very severe, few if any apples may set in such a cluster, or, if they do set, they are likely to drop early.

Not only does the rosy apple aphis attack the flower clusters, but in severe infestations it may spread over the entire foliage, tho generally most of the injury is low down in the tree around the outer margin. The leaves become badly curled, forming tight rolls within which myriads of lice are at work and from which migrations to the surrounding foliage constantly occur (Plates XIII and XIV).

This species probably does the severest damage to the fruit of any of the three species discussed in this paper. Parrott (1916 and 1917) performed some interesting experiments on the inhibition of growth of the fruit due to the attacks of the three species. He found that the greatest inhibition of growth, in both axial and transverse diameters of the fruit, was due to the attacks of the rosy aphis. Fruits that have been injured are usually elongate, puckered at the calyx end, and somewhat distorted (Plates XV–XVII). If not too badly injured, such fruits cling to the tree, growing but slightly and giving the so-called "cluster apples" at picking time. These cluster apples consist usually of from four to seven apples on a spur, which are small, distorted, and knotty. In a badly infested orchard, cluster apples may form the majority of the fruit at picking time.

THE APPLE-BUD APHIS

Since the species *Aphis avenae* hatches from a week to ten days earlier than the other two species, it is the first one found on the bursting buds. When abundant, as is frequently the case, it may almost completely cover the buds. As the buds open, the young lice swarm over the leaves but never cause them to curl. Since in this vicinity practically all of the descendants of the stem mothers become winged and leave for their summer host plants, they do scarcely any serious damage to either the foliage, the fruit, or the developing shoots.

THE APHIS SITUATION DURING THE LAST OF JUNE EACH YEAR

Before closing the discussion of injury to the apple, a summary of the situation during the latter part of June may be worthy of consideration.

At this period the aphis situation is usually a serious one for the orchardist, especially if he has not sprayed to control the lice and if the predacious and parasitic enemies of plant lice are not present in very considerable numbers. The factors determining the numbers and activities of the enemies of plant lice are many and are extremely complicated. No experimental work has been done on this phase of the problem, and up to this time only general statements based on field observations occur in the literature. With adequate facilities, two factors — temperature and moisture — might be studied. It is almost certain that these two factors are the controlling ones, but how they act has not been determined.

The reproductive capacity tables show that during the latter half of June the stem mothers probably cease reproducing and most of them die. The second and third generations are reproducing at their maximum, and the fourth generation of *Aphis pomi* will reach its maximum about the last days of June. It will thus be seen that if the parasitic and predacious enemies have not kept pace with their hosts, the severest injury may occur during the latter half of June. This is what occurs in an aphis year, and the reason for it can readily be seen by consulting the reproductive capacity tables. During the remainder of the summer, from July 1, the numbers of plant lice generally decrease, and this despite the fact that young of *Aphis pomi* are being produced in countless millions. The season has now become warm, a condition apparently most favorable for parasitic and predacious enemies, and these are able to gain the upper hand.

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PART I. DISTRIBUTION AND TAXONOMY OF THE ADULT FLIES[1]

CHARLES PAUL ALEXANDER

The crane-fly fauna of New York State may be considered as representative of that of northeastern North America. For more than half a century New York has been one of the favorite collecting grounds for students of this neglected group of insects. The original plan of the present paper was to include only the species that are actually known to occur in this State. However, it should be understood and appreciated that in groups of insects which have been long ignored by almost all students of entomology, such as the group under consideration, it is still impossible to give the exact range of any particular species, and forms that seem to be confined to certain sections of the country upset all calculations by reappearing in distant regions which had been considered as far outside the range of the species. Thus it is possible that almost any species occurring in northeastern America may be found within the limits of this State, altho some species are now known only from localities so distant as to make it seem improbable that they may be found here also. For this reason the scope of the present paper has been extended to include the northeastern United States and eastern Canada — Labrador and Newfoundland, south to Virginia and Kentucky, west to Iowa, Minnesota, and Manitoba. It is believed that this area includes about all of the local probabilities, but there are undoubtedly new species yet to be discovered and lost species to be recognized.

The number of species of crane-flies that should occur in New York State is probably not less than three hundred, and this figure seems similarly applicable to many areas of equal extent and equal diversity of ecological conditions in the North Temperate Zone.

The student of this group of flies will find that there is still very much to be done in determining the exact seasonal and geographical distribution

[1] This study was conducted in the entomological laboratory of Cornell University, under the direction of Dr. James G. Needham, Dr. J. Chester Bradley, and Dr. O. A. Johannsen, to whom the writer is indebted for many helpful criticisms and suggestions.

of the species here included. Present knowledge of the biology and ecology of these species, and exact data on the duration of the different periods of the immature stages, are still very meager, and it is this field more than any other that offers the greatest opportunities for research.

The classification herein adopted is that of Osten Sacken, but it may be well to state that very many fundamental changes are to be expected when the immature stages are better known.

In the course of the author's studies on the local Tipulidae, it was necessary for him to visit and examine most of the important collections in the East. In some cases in which it was impracticable to visit the museums, specimens were lent by the authorities in charge. The writer wishes to express his gratitude to the persons who kindly assisted in this manner. Among the collections studied were those contained in the following institutions:

United States National Museum, Washington, D. C. This museum contains probably the largest collection of crane-flies in the New World, including the types of Coquillett and the Limnobiinae described by Doane, as well as much of the material determined by the author. The collection was examined on several occasions thru the kindness of the late Mr. Frederick Knab, custodian of the Diptera.

United States Biological Survey, Washington, D. C. The collections here, examined thru the kindness of Mr. W. L. McAtee, are extensive, and are particularly rich in local forms and in material from the Pribilof Islands.

Museum of Comparative Zoology, Cambridge, Massachusetts. These collections, examined on several occasions thru the kindness of the Director, Mr. Samuel Henshaw, include the types of Osten Sacken and Loew and are of the greatest importance on that account. The material is in a fine state of preservation because of the constant care given to it.

Boston Society of Natural History, Boston, Massachusetts. These collections, examined thru the kindness of the Curator, Mr. Charles W. Johnson, are very fine, almost complete as far as the New England fauna is concerned, and of great value to the student. The type of *Chionea valga* Harris, as well as many of Say's species and the specimens determined by him, are to be found here.

Academy of Natural Sciences, Philadelphia, Pennsylvania. The material here includes the collections of the American Entomological Society. The collections were examined thru the kindness of Mr. E. T. Cresson, jr. They include the type of *Triogma exculpta* Osten Sacken, and cotypes of many of the other Sackenian species as well as a good representation of other forms.

American Museum of Natural History, New York City. This rather considerable collection, examined thru the kindness of Dr. F. E. Lutz, includes many of Williston's cotypes and is especially rich in Antillean and South American forms.

Museum of the Brooklyn Institute, Brooklyn, New York. This collection was examined thru the kindness of the custodian, Mr. Charles Shaeffer. It is a rather small local collection, but the specimens have been authoritatively determined by Johnson and they form a good nucleus for future work.

New York State Museum, Albany, New York. This is a good local collection, examined on several occasions thru the kindness of the State Entomologist, Dr. E. P. Felt, and the assistant entomologist, Mr. D. B. Young.

Cornell University, Ithaca, New York. This collection is under the direction of Dr. James G. Needham and Dr. J. Chester Bradley. It is a very complete collection, including many specimens taken in the seventies by Professor J. H. Comstock and the late Mr. H. H. Smith and determined by Osten Sacken. The type of *Rhabdomastix flava* is here.

Maine Agricultural Experiment Station, Orono, Maine. This is a very good local collection, made in large part by the author in 1913, under the employment of the Director, Dr. Charles D. Woods, and the Station Entomologist, Dr. Edith M. Patch.

Department of Entomology of North Carolina, Raleigh, North Carolina. This collection was examined thru the kindness of the State Entomologist, Mr. Franklin Sherman, and Mr. R. W. Leiby. It is a good collection of local material.

Ohio State University, Columbus, Ohio. This collection was examined thru the kindness of Professor James Hine, who collected the greater part of the material.

University of Minnesota, St. Paul, Minnesota. This is a good local collection, including most of the material mentioned in Washburn's *Diptera of Minnesota.* It was sent to the writer by Mr. Simon Marcovitch. Considerable additional material from the region of Lake Itasca was given to the writer for determination by the collector, Mr. Samuel A. Graham.

Washington State Agricultural College, Pullman, Washington. This collection is very important, as it contains many of the Tipulinae described by Doane. The writer was unable to visit the collection, but Dr. Axel L. Melander very kindly sent him the cotype specimens of three or four eastern species that were needed in the preparation of this paper.

Canadian National Museum, Ottawa, Ontario. This collection was sent to the writer for naming, thru the kindness of the Dominion Entomologist, Dr. C. Gordon Hewitt. It is a rather extensive collection, from most parts of the Dominion.

University of Toronto, Toronto, Ontario. This is a small collection, mostly taken by Dr. E. M. Walker and including the types of *Phalacrocera neoxena.* It contains also a few additional specimens collected by Dr. W. A. Clemens and including the type of *Tipula algonquin.*

New Brunswick Experiment Station, Fredericton, New Brunswick. This is a good local collection, taken by the Station Entomologist, Mr. John D. Tothill.

Nova Scotia Experiment Station, Truro, Nova Scotia. This is a very good local collection, taken by Dr. Robert Matheson. It is now in the collection at Cornell University.

In addition to the public collections listed above, there are in the United States a few private collections of great value, as follows:

The collection of Dr. W. G. Dietz, Hazleton, Pennsylvania. This is a very considerable collection of North American species, including the types of the species described by the owner.

The collection of Mr. C. W. Johnson, Boston, Massachusetts. This is an exceptionally fine collection, and includes the types of many of the species described by the owner.

The collection of Dr. J. G. Needham, Ithaca, New York. This is a good local collection, mounted in balsam. It includes the types of *Dicranomyia whartoni* and *Dolichopeza americana.*

The collection of Mr. M. C. Van Duzee, Buffalo, New York. This collection is very rich in local and Floridian species, and includes the type of *Geranomyia vanduzeei.*

The collection of the author, Urbana, Illinois. This includes a good representation of local forms and many extra-limital species. The types of many of the species described by the author are in this collection.

In addition to those named above, there have been examined several collections made by students in systematic entomology at Cornell University during the past few years. The more notable of these are the collections of Dr. W. T. M. Forbes, and Messrs. J. T. Lloyd, S. W. Frost, E. A. Richmond, W. C. Woods, and Hachiro Yuasa. The following very considerable collections, made in different parts of the country, have been of great value in determining the range of North American species:

The two Beutenmüller collections, one in the American Museum and the other in the collection of Dr. Dietz, from the Black Mountains, North Carolina.

The Nathan Banks collections, from the same locality and from northern Virginia.

The Karl P. Schmidt collection, made in Louisiana.

The J. Chester Bradley collections, made in Georgia, New York, and the West.

The R. C. Shannon collections, from the vicinity of Washington, D. C.

The Axel Olsson collections, from North Carolina and New York.

The H. H. Knight collections, from western New York.

The H. M. Parshley collections, from Maine and Massachusetts.

The Cordelia Stanwood collections, from Hancock County, Maine.

Collections made in the vicinity of Georgian Bay, Ontario, by Dr. W. A. Clemens in 1912, by Mrs. John D. Tothill in 1914, and especially by Mr. H. S. Parish in 1915.

The Bryant Newfoundland specimens in the collection of Mr. Johnson.

Material from near Washington, D. C., and from Maine, collected by Mr. W. L. McAtee.

The Ely (Connecticut) and Weidt (New Jersey) material in the collection of Dr. Dietz.

The extensive collections made in Bergen County, New Jersey, by Mr. M. D. Leonard.

Specimens collected by Oslar (Colorado), Munz (Colorado), and Woodgate (New Mexico), and other material in the collection of the author.

To all the above-mentioned persons the author expresses his sincere gratitude for the privilege of seeing these specimens and obtaining the records.

In addition to the collections that the writer has been able to visit, there are several others of high repute — the collection in the Carnegie Museum (Pittsburg, Pennsylvania), the private collection of Mr. Charles Dury (Cincinnati, Ohio), the collections of the Illinois State Laboratory of Natural History and the University of Michigan, and others —

which unquestionably will supply many new, chiefly local, records when their contents are made known.

SYSTEMATIC POSITION OF THE SPECIES

The families that make up the insects known as crane-flies are four in number — the Tanyderidae, the Ptychopteridae, the Rhyphidae, and the Tipulidae. All but the last-named of these families are very limited in number of species, the total number of described forms being not far in excess of threescore. Crane-flies belong to the division Nematocera of the suborder Orthorrhapha. They are characterized by having six or more segments in the elongated antennae. The only families of flies with which crane-flies might be confused are the Bibionidae and the Dixidae.

Crane-flies are very often of large size. They are the largest of the Nematocera and are among the largest of all Diptera. The differences in size found in the family Tipulidae are very great, ranging from the giants of the family, *Ctenacroscelis praepotens*, *Tipula brobdinagia*, and others, down to such species as *Erioptera parva* and *Molophilus ursinus*, veritable pygmies. In the area considered in this paper, the largest species found are *Longurio testaceus* and *Tipula abdominalis*, and the smallest is *Molophilus ursinus*.

In appearance crane-flies may be described as mosquito-like and they are very often mistaken for mosquitoes, the larger species often causing great alarm. There are no crane-flies, however, that have the biting habits of the Culicidae. The legs of all crane-flies are long and slender, in some cases being exceedingly so, and this feature has given most of the common names that are applied to these insects — crane-flies, daddy longlegs, and the like. The wings are many-veined (polyneura), and in most species they possess a completely inclosed discal cell (*1st* M_2). In all Tipulidae and in the trichocerine Rhyphidae there are two anal veins, a character never possessed by the more specialized Nematocera. On the mesonotum there is a distinct, more or less transverse, V-shaped suture separating the prescutum from the scutum. In the Tanyderidae, the Ptychopteridae, and the Rhyphidae this suture is rather poorly defined. Ocelli are found only in the Rhyphidae. The large size, the inclosed discal cell, the presence of two anal veins, and the V-shaped suture, are sufficient to distinguish the local species of Tipulidae.

ECONOMIC IMPORTANCE

Economically, crane-flies are found to play a relatively important rôle. The adult flies are entirely harmless, but the larvae of many species are destructive to various crops. In Europe the best-known of such species is *Tipula oleracea* Linn. In eastern North America the smoky crane-fly, *T. cunctans* Say (called *T. infuscata* Loew by Hyslop, 1910[2]), working principally on leguminous species, and *T. bicornis* Forbes working largely on grasses, often become serious pests; in the West the alfalfa crane-fly, *T. simplex* Doane (Essig, 1913), is often of exceedingly great importance, working on various legumes and grass species. Other species, as *T. derbyi* Doane and *T. aspidoptera* Alex., often do considerable local damage. In Japan, *T. longicauda* Mats. and a species that has been determined as *T. parva* Loew do very considerable damage to rice and sugar cane. It is to be noted that all these more destructive species belong to the tribe Tipulini, comprising the larger species of crane-flies, and the damage is done by the larvae's feeding on the roots and thus causing the death of the plants.

The species of Tanyptera live in logs or stumps that are fairly sound and free from decay. The larvae of some species of Rhipidia, Limnobia, Trichocera, and other genera, affect stored roots and tubers. The species of Ula and some species of Limnobia live in fungi (Boletus, Armillaria, Hypomyces, and others), and in some cases may be of economic importance in mushroom culture.

As an element of food for vertebrates, crane-flies occupy a prominent position. The records of Dr. Dallas Hanna and those of the Whitneys, in the possession of the United States Biological Survey, state that larvae representing an unknown species of Tipula are abundant everywhere thruout the summer season on St. Paul Island, of the Pribilof group in Bering Sea. These larvae are found around the roots of grasses and herbs, and especially under beds of moss, on the roots of which they feed, killing the moss over considerable areas. Under such a moss bed as many as twenty larvae to the square foot have been collected. The larvae must be of considerable ecological importance because of their food value to birds and foxes. Foxes will dig over large areas of moss beds to feed on them. Thruout the arctic regions the family Tipulidae

[2] Dates in parenthesis refer to *References cited*, page 959.

seems very abundant, both in number of species and in number of individuals, and the larvae are exceedingly numerous.

The Biological Survey has kept a very careful record of the food of birds and other vertebrates, based on the examination of stomach contents, and thru the kindness of Messrs. W. L. McAtee and E. R. Kalmbach the writer has obtained a record of the species known to feed on crane-flies. Over a hundred species of birds, representing almost all the bird families, have been found to feed on the adult flies. The more notable and general of these birds are sandpipers, flycatchers, vireos, swallows, wood warblers, and thrushes. The species feeding on the larvae consist for the most part of ducks, shore birds, and thrushes. Dr. Alice A. Noyes has found in the stomach of a Wilson's snipe twenty-three head capsules of a small Tipula (possibly *T. dejecta* Walker), showing the importance of the larvae as food at certain seasons. Similarly the food of toads (Bufo) and of frogs (Rana) often includes an abundance of larval and adult crane-flies (Needham, 1905).

The larvae of crane-flies are very tempting to many species of fishes. Certain of the larger larvae, such as those of *Tipula abdominalis* and *Eriocera spinosa,* furnish one of the best of baits for black bass and other game fish, being even more tempting in many cases than the better-known dobson (Corydalis). The skin of these larvae is very tough and leathery, hence their common name *leather-jacket.* The fishhook is run thru the body of the larva at about midlength, leaving the two ends wriggling. Studies made by Needham (1908:172–188) on the food of the bullhead, the sunfish, and the red-bellied minnow, showed that crane-flies were not eaten by these species, and the same is true of the brook trout in ponds (Needham, 1903 a). But the habitat of the larvae is not in the haunts of these fishes. They live in the leaf drift caught in the eddies, in the mud and gravel at the sides and the bottom of the stream, and in similar situations which are not readily accessible to the fish. It seems probable that it is due to the fact that the larvae furnish such choice titbits, that they cannot exist in the same haunts with the fish. Some species, as those of Eriocera, live in the chutes of the Mississippi River, and they are the only crane-flies known from such a habitat. The remains of crane-flies, such as wings, legs, and heads, are often found in fish stomachs, these being from adult flies that have fallen into the water and been snapped up by the fish.

DISTRIBUTION

GEOLOGICAL DISTRIBUTION

The source of origin of the crane-flies is still largely problematical, but the preponderance of evidence now seems to indicate that they came from some neuropteroid ancestor far back in Mesozoic times. This is expressed by Needham (1908:221) as follows: "The suggestion has been made before by others, and I think it very possible, that some Panorpidlike neuropteroid mutant got its center of gravity hitched forward, its hind wings reduced, and started the dipterous line of evolution."

The first insects that can be definitely referred to the Tipulidae appeared rather suddenly in late Mesozoic times. They belong almost entirely to the subfamily Tipulinae, but the records are very scanty and for the most part unsatisfactory. The evidence that specimens of Tanyderidae, Ptychopteridae, or Limnobiinae occurred at that time is very doubtful. In the Tertiaries, however, the group was extraordinarily developed and it seems quite possible that the family reached its maximum of diversity in the Miocene period or a little later and is now a waning group. From the Oligocene period of British Columbia, Handlirsch (1910) has recorded a curious tanyderid under the name *Etoptychoptera*. The Florissant beds of Colorado were laid down in a lake that is supposed to be of the late Oligocene or the early Miocene age. There have been taken from these beds hundreds if not thousands of specimens, representing about seventy-five species, indicating the extreme richness of the crane-fly fauna during that age. On one slab of the deposit Scudder found a specimen of his *Dicranomyia inferna* which was partly overlain by a specimen of his *D. fontainei*, a condition very suggestive of the remarkable richness of this fauna. The abundance of species in the amber fauna, likewise of the Tertiaries, was indicated by Loew in 1850 and more recently elaborated by Meunier. The present knowledge of the Florissant fauna is due to the work of Scudder, Cockerell, and Wickham.

GEOGRAPHICAL DISTRIBUTION

A summary of the crane-fly fauna of the world

The four families comprising the crane-flies are represented in almost every part of the world where life is possible. Apparently the range of the group is restricted only by great extremes of temperature.

The lesser oceanic islands (the Seychelles, the Fiji, the Hawaiian, and others) that have been at all studied are quite devoid of species of the subfamily Tipulinae, these species being of large size and often possessing considerable powers of flight; while the much smaller species in the Limnobiinae are often very numerous and may include a considerable range of species. Crane-flies in the arctic regions are very abundant and are represented by a few genera of Limnobiinae and many species of Tipula. Many of the latter have the wings atrophied so that they are incapable of flight. This condition is particularly true of forms along the coast or on wind-swept islands adjoining the mainland, and may be confined to the female sex alone or may be found in both sexes. It must be understood, however, that reduction of the wings is by no means confined to such environments or to the genus Tipula, since it occurs in almost all the major groups of crane-flies — in Limnobiini (Zalusa End.), Eriopterini (Platylimnobia Alex., Chionea Dalm.), Limnophilini (Zaluscodes Lamb, Alfredia Bezzi, *Limnophila aspidoptera* Coq.), Pediciini (*Tricyphona hannai* Alex.), and many others—and is found in many different parts of the world tho usually in arctic, oceanic, or mountainous situations. *Tipula besselsi* O. S., described from Polaris Bay, northern Greenland, is found above the 80th degree of north latitude and within a few hundred miles of the North Pole.

The four families of crane-flies include, respectively, the following numbers of genera, subgenera, and species:[3]

	Genera	Subgenera	Species
TANYDERIDAE	2	....	8
PTYCHOPTERIDAE:			
Ptychopterinae	1	....	12
Bittacomorphinae	2	....	4
RHYPHIDAE:			
Trichocerinae	2	2	22
Rhyphinae	3	....	26
Mycetobiinae	2	....	7
TIPULIDAE:			
Limnobiinae:			
Limnobiini	10	5	365
Antochini	15	1	160
Eriopterini	28	10	410
Limnophilini	16	10	290

[3] This table is dated June 1, 1916.

	Genera	Subgenera	Species
TIPULIDAE (*continued*):			
Limnobiinae (*continued*):			
Hexatomini	4	....	125
Pediciini	7	3	75
Cylindrotominae	5	....	16
Tipulinae:			
Dolichopezini	9	2	45
Ctenophorini	7	....	50
Tipulini	21	3	900
Total	134	36	2,515

The Tanyderidae have two living genera, one antipodal and the other (Protoplasa) with two Nearctic species.

The Ptychopteridae have three genera. One of these, Ptychoptera, is found in most parts of the world excepting Australasia, while the other two, Bittacomorpha and Bittacomorphella, are Nearctic.

The Rhyphidae have seven genera, arranged in three subfamilies. The species, with few exceptions, are from the North Temperate Zone.

Among the Tipulidae, the tribes Limnobiini, Antochini, Eriopterini, Limnophilini, Dolichopezini, Ctenophorini, and Tipulini are almost cosmopolitan. The tribe Hexatomini has the genus Hexatoma dominant in Europe, and the genus Eriocera cosmopolitan except for the Palaearctic and Australasian regions. The tribe Pediciini reaches its greatest development in the North Temperate Zone. The Cylindrotominae are holarctic, with one genus (Stibadocera) occurring in the Oriental region.

Lists of the species of adjoining States and provinces

The following lists of species are given to supplement the data on the New York fauna.

Maine

The data for Maine are based largely on the results obtained by the author from a study of the group during a period of fifteen weeks, under the direction of Dr. Charles D. Woods and Dr. Edith M. Patch. Very valuable collections in this State have been made by Mr. Charles W. Johnson, Miss Cordelia J. Stanwood, Dr. H. M. Parshley, Professor Herbert Osborn, Professor A. P. Morse, and others.

Ptychoptera rufocincta O. S.

Bittacomorpha clavipes (Fabr.)

Bittacomorphella jonesi (Johns.)

Trichocera regelationis (Linn.)

Discobola argus (Say)

Dicranomyia badia (Walk.)
gladiator O. S.
globithorax O. S.
haeretica O. S.
halterata O. S.
immodesta O. S.
liberta O. S.
longipennis (Schum.)
morioides O. S.
pubipennis O. S.
pudica O. S.
rostrifera O. S.
simulans (Walk.)

Geranomyia diversa O. S.
rostrata (Say)

Limnobia cinctipes Say
hudsonica O. S.
immatura O. S.
indigena O. S.
parietina O. S.
solitaria O. S.
triocellata O. S.
tristigma O. S.

Rhipidia bryanti Johns.
maculata Meig.

Antocha saxicola O. S.

Elephantomyia westwoodi O. S.

Rhamphidia mainensis Alex.

Toxorhina muliebris (O. S.)

Cladura flavoferruginea O. S.

Cryptolabis paradoxa O. S.

Erioptera armata O. S.
armillaris O. S.
caloptera Say
chlorophylla O. S.
chrysocoma O. S.
needhami Alex.
septemtrionis O. S.
stigmatica (O. S.)
straminea O. S.
venusta O. S.
vespertina O. S.

Gnophomyia tristissima O. S.

Gonomyia florens Alex.
subcinerea O. S.

Molophilus comatus (Doane)
hirtipennis (O. S.)
pubipennis (O. S.)

Ormosia monticola (O. S.)
nigripila (O. S.)
nubila (O. S.)
pygmaea (Alex.)
rubella (O. S.)

Helobia hybrida (Meig.)

Adelphomyia americana Alex.
cayuga Alex.
minuta Alex.

Epiphragma fascipennis (Say)

Limnophila adusta O. S.
areolata O. S.
brevifurca O. S.
fasciolata O. S.
fuscovaria O. S.
inornata O. S.
lenta O. S.
luteipennis O. S.
macrocera (Say)
montana O. S.
munda O. S.
nigripleura A. & L.
novae-angliae Alex.
noveboracensis Alex.
osborni Alex.
quadrata O. S.
recondita O. S.
rufibasis O. S.
stanwoodae Alex.
tenuicornis O. S.
tenuipes (Say)
toxoneura O. S.
ultima O. S.
unica O. S.

Ula elegans O. S.

Ulomorpha pilosella (O. S.)

Eriocera longicornis (Walk.)
spinosa (O. S.)

Pedicia albivitta Walk.

Rhaphidolabis cayuga Alex.
flaveola O. S.
tenuipes O. S.

Tricyphona autumnalis Alex.
calcar (O. S.)
inconstans (O. S.)
katahdin Alex.
vernalis (O. S.)

Cylindrotoma americana O. S.

Liogma nodicornis (O. S.)

Phalacrocera tipulina O. S.

Dolichopeza americana Needm.

Oropeza dorsalis Johns.
obscura Johns.
sayi Johns.
venosa Johns.

Ctenophora apicata O. S.

Nephrotoma eucera (Loew)
ferruginea (Fabr.)
incurva (Loew)
lugens (Loew)
pedunculata (Loew)
punctum (Loew)
sodalis (Loew)
tenuis (Loew)
vittula (Loew)
xanthostigma (Loew)

Stygeropis fuscipennis Loew

Tipula abdominalis (Say)
algonquin Alex.
angulata Loew
angustipennis Loew
apicalis Loew
bella Loew
bicornis Forbes
caloptera Loew
cayuga Alex.
cunctans Say
fragilis Loew
hebes Loew
hermannia Alex.
longiventris Loew
macrolabis Loew
mainensis Alex.
nobilis (Loew)
oropezoides Johns.
parshleyi Alex.
penobscot Alex.
sayi Alex.
senega Alex.
serta Loew
strepens Loew
submaculata Loew
sulphurea Doane
tephrocephala Loew
trivittata Say
ultima Alex.
valida Loew

New Brunswick

(The collections of the New Brunswick Experiment Station, made by Mr. John D. Tothill and others)

Bittacomorpha clavipes (Fabr.)

Dicranomyia morioides O. S.

Geranomyia canadensis (Westw.)

Limnobia cinctipes Say

Erioptera armata O. S.

Limnophila adusta O. S.
imbecilla O. S.
inornata O. S.
quadrata O. S.
recondita O. S.
rufibasis O. S.

Eriocera longicornis (Walk.)

Liogma nodicornis (O. S.)

Oropeza sayi Johns.
venosa Johns.

Ctenophora apicata O. S.

Nephrotoma eucera (Loew)
ferruginea (Fabr.)
incurva (Loew)
lugens (Loew)
occipitalis (Loew)
pedunculata (Loew)
tenuis (Loew)
xanthostigma (Loew)

Tipula abdominalis (Say)
angulata Loew
angustipennis Loew
caloptera Loew
eluta Loew
hebes Loew
latipennis Loew
macrolabis Loew
parshleyi Alex.

Tipula strepens Loew
sulphurea Doane
tephrocephala Loew
ternaria Loew
Tipula trivittata Say
ultima Alex.
valida Loew

Nova Scotia

(The collections of Dr. Robert Matheson, of Cornell University)

Ptychoptera rufocincta O. S.

Bittacomorpha clavipes (Fabr.)

Trichocera bimacula Walk.

Dicranomyia haeretica O. S.
halterata O. S.
immodesta O. S.
liberta O. S.

Rhipidia maculata Meig.

Limnobia solitaria O. S.
triocellata O. S.

Discobola argus (Say)

Antocha saxicola O. S.

Elephantomyia westwoodi O. S.

Erioptera armata O. S.
armillaris O. S.
caloptera Say
chlorophylla O. S.
septemtrionis O. S.

Gonomyia mathesoni Alex.
sulphurella O. S.

Rhabdomastix flava (Alex.)

Cryptolabis paradoxa O. S.

Limnophila adusta O. S.
lenta O. S.
macrocera (Say)
noveboracensis Alex.
recondita O. S.
tenuicornis O. S.
toxoneura O. S.

Pedicia albivitta Walk.
contermina Walk.

Tricyphona inconstans (O. S.)
vernalis (O. S.)

Eriocera longicornis (Walk.)
spinosa (O. S.)

Liogma nodicornis (O. S.)

Tanyptera frontalis (O. S.)

Nephrotoma eucera (Loew)
ferruginea (Fabr.)
incurva (Loew)
lugens (Loew)
macrocera (Say)
pedunculata (Loew)
tenuis (Loew)

Tipula abdominalis (Say)
angustipennis Loew
apicalis Loew
bella Loew
caloptera Loew
cayuga Alex.
fragilis Loew
hebes Loew
hermannia Alex.
parshleyi Alex.
sayi Alex.
submaculata Loew
tephrocephala Loew
tricolor Fabr.
trivittata Say
ultima Alex.
valida Loew

Quebec

The published list for Quebec (Winn and Beaulieu, 1915) has been revised, certain species being dropped, a few others added, and certain parts of the synonymy corrected. The record for *Dicranomyia distans* O. S., an Austral species ranging as far north as Washington, D. C., is evidently erroneous. The species of Trichocera and Tanyptera are

given as determined by C. W. Johnson. Our knowledge of the crane-flies of Quebec is due to the work of Beaulieu, Beaulne, Chagnon, Couper, Fyles, Winn, and others.

Ptychoptera rufocincta O. S.

Bittacomorpha clavipes (Fabr.)

Trichocera maculipennis (Fabr.)
regelationis (Linn.)

Dicranomyia immodesta O. S.
liberta O. S.
longipennis (Schum.)
pudica O. S.

Limnobia cinctipes Say
indigena O. S.
solitaria O. S.
tristigma O. S.

Rhipidia maculata Meig.

Discobola argus (Say)

Antocha saxicola O. S.

Elephantomyia westwoodi O. S.

Rhamphidia flavipes Macq.

Chionea valga Harr.

Ormosia monticola (O. S.)

Erioptera armata O. S.
armillaris O. S.
caloptera Say
chlorophylla O. S.
chrysocoma O. S.
septemtrionis O. S.
venusta O. S.
vespertina O. S.

Molophilus pubipennis (O. S.)

Gonomyia subcinerea O. S.

Gnophomyia tristissima O. S.

Helobia hybrida (Meig.)

Epiphragma fascipennis (Say)

Limnophila adusta O. S.
areolata O. S.
brevifurca O. S.
contempta O. S.
fuscovaria O. S.
imbecilla O. S.
macrocera (Say)
montana O. S.

Limnophila munda O. S.
quadrata O. S.
rufibasis O. S.
tenuipes (Say)
toxoneura O. S.
ultima O. S.

Pedicia albivitta Walk.

Tricyphona autumnalis Alex.
inconstans (O. S.)

Liogma nodicornis (O. S.)

Oropeza albipes Johns.
obscura Johns.

Ctenophora apicata O. S.

Tanyptera atrata (Linn.)
dorsalis (Walk.)
fumipennis (O. S.)
topazina (O. S.)

Nephrotoma eucera (Loew)
ferruginea (Fabr.)
incurva (Loew)
lineata (Scop.)
lugens (Loew)
occipitalis (Loew)
sodalis (Loew)
tenuis (Loew)
xanthostigma (Loew)

Stygeropis fuscipennis Loew

Tipula abdominalis (Say)
angulata Loew
angustipennis Loew
bella Loew
bicornis Forbes
caloptera Loew
cincticornis Doane
collaris Say
dejecta Walk.
eluta Loew
grata Loew
hebes Loew
hermannia Alex.
iroquois Alex.
latipennis Loew
macrolabis Loew
megaura Doane
retorta v. d. W.

Tipula sayi Alex.
senega Alex.
serta Loew
sulphurea Doane
tephrocephala Loew
Tipula trivittata Say
ultima Alex.
umbrosa Loew
valida Loew
vitrea v. d. W.

Newfoundland

(The Owen Bryant collections in the cabinet of C. W. Johnson)

Bittacomorpha clavipes (Fabr.)

Erioptera chlorophylla O. S.

Limnophila rufibasis O. S.
terrae-novae Alex.

Tricyphona inconstans (O. S.)

Nephrotoma vittula (Loew)

Tipula abdominalis (Say)
hermannia Alex.
mainensis Alex.
trivittata Say
umbrosa Loew
valida Loew

Labrador

(Many of the types of Loew and Alexander, collected by Packard, Schneider, and Bryant)

Dicranomyia halterata O. S.

Tricyphona hyperborea (O. S.)

Dolichopeza americana Needm.

Tipula angustipennis Loew
imperfecta Alex.
labradorica Alex.
septentrionalis Loew

Washington, D. C., and vicinity

This remarkable local list is added here to indicate the southern species that may range into our limits. The pioneer collecting of Osten Sacken has been thoroly supplemented by that of W. L. McAtee, R. C. Shannon, Frederick Knab, and some others.

Ptychoptera rufocincta O. S.

Bittacomorpha clavipes (Fabr.)

Bittacomorphella jonesi (Johns.)

Trichocera sp.

Discobola argus (Say)

Dicranomyia badia (Walk.)
brevivena O. S.
distans O. S.
diversa O. S.
floridana O. S.
gladiator O. S.
globithorax O. S.
haeretica O. S.
immodesta O. S.
liberta O. S.

Dicranomyia macateei Alex.
morioides O. S.
pubipennis O. S.
rara O. S.
simulans (Walk.)

Geranomyia canadensis (Westw.)
rostrata (Say)

Limnobia cinctipes Say
immatura O. S.
indigena O. S.
triocellata O. S.
tristigma O. S.

Rhipidia bryanti Johns.
domestica O. S.
fidelis O. S.
maculata Meig.
shannoni Alex.

Antocha saxicola O. S.

Atarba picticornis O. S.

Elephantomyia westwoodi O. S.

Dicranoptycha sobrina O. S.
winnemana Alex.

Rhamphidia flavipes Macq.
mainensis Alex.

Teucholabis complexa O. S.
lucida Alex.

Toxorhina muliebris (O. S.)

Cladura flavoferruginea O. S.

Erioptera armata O. S.
armillaris O. S.
caloptera Say
chlorophylla O. S.
chrysocoma O. S.
graphica O. S.
needhami Alex.
noctivagans Alex.
parva O. S.
septemtrionis O. S.
venusta O. S.
vespertina O. S.

Gnophomyia luctuosa O. S.
tristissima O. S.

Gonomyia blanda O. S.
cognatella O. S.
manca (O. S.)
subcinerea O. S.
sulphurella O. S.

Helobia hybrida (Meig.)

Molophilus hirtipennis (O. S.)
nova-caesariensis Alex.
pubipennis (O. S.)
ursinus (O. S.)

Ormosia holotricha (O. S.)
innocens (O. S.)
nigripila (O. S.)
nubila (O. S.)

Trimicra anomala O. S.

Adelphomyia americana Alex.

Epiphragma fascipennis (Say)
solatrix (O. S.)

Limnophila adusta O. S.
aprilina O. S.
areolata O. S.

Limnophila brevifurca O. S.
contempta O. S.
emmelina Alex.
fuscovaria O. S.
lenta O. S.
luteipennis O. S.
macrocera (Say)
montana O. S.
mundoides Alex.
nigripleura A. & L.
quadrata O. S.
recondita O. S.
rufibasis O. S.
tenuipes (Say)
terebrans Alex.
toxoneura O. S.
ultima O. S.

Ula paupera O. S.

Eriocera cinerea Alex.
fuliginosa O. S.
longicornis (Walk.)
tristis Alex.
wilsonii O. S.

Hexatoma megacera (O. S.)

Penthoptera albitarsis O. S.

Dicranota eucera O. S.
noveboracensis Alex.
rivularis O. S.

Pedicia albivitta Walk.

Rhaphidolabis tenuipes O. S.

Tricyphona inconstans (O. S.)
vernalis (O. S.)

Liogma nodicornis (O. S.)

Brachypremna dispellens (Walk.)

Oropeza albipes Johns.
dorsalis Johns.
obscura Johns.
sayi Johns.
subalbipes Johns.

Tanyptera frontalis (O. S.)

Longurio testaceus Loew

Nephrotoma eucera (Loew)
ferruginea (Fabr.)
incurva (Loew)
macrocera (Say)
occipitalis (Loew)
polymera (Loew)
tenuis (Loew)

Nephrotoma virescens (Loew)
xanthostigma (Loew)

Tipula abdominalis (Say)
annulicornis Say
australis Doane
bella Loew
bicornis Forbes
caloptera Loew
collaris Say
cunctans Say
dejecta Walk.
dietziana Alex.
eluta Loew
fragilis Loew
fraterna Loew
fuliginosa (Say)

Tipula hebes Loew
hermannia Alex.
ignobilis Loew
iroquois Alex.
johnsoniana Alex.
longiventris Loew
mingwe Alex.
morrisoni Alex.
perlongipes Johns.
sayi Alex.
submaculata Loew
tricolor Fabr.
triton Alex.
trivittata Say
tuscarora Alex.
ultima Alex.
umbrosa Loew

The crane-flies of New York

The fact that New York has a known crane-fly fauna which is larger and better-developed than that of any other State in the Union, is due, in large part, to the diversity of natural conditions, which range from high mountains to sea level and include lakes, rivers, swamps, bogs, woodlands, gorges, ravines, and most other haunts that attract these insects. Another reason for this exceptional list is the fact that the State has long been a favorite collecting ground for many students of crane-flies, and a large number of species were first characterized from material taken in New York. These include species described by Osten Sacken, Loew, Doane, Johnson, Needham, Dietz, and Alexander. The pioneer collector, Baron Osten Sacken, did much of his collecting in this State, especially in the Adirondacks at Trenton Falls, in the Schoharie Valley at Sharon Springs, in the vicinity of New York City, and later in the Catskills. His work furnished the basis for Needham's preliminary list (Needham, 1908:203–211), which includes one hundred and four species known from New York at that time. Subsequent collecting in various parts of the State has considerably increased the number of species, so that comparatively few additions may be expected. The more probable of these have been indicated in the following list under the heading *Regional species.*

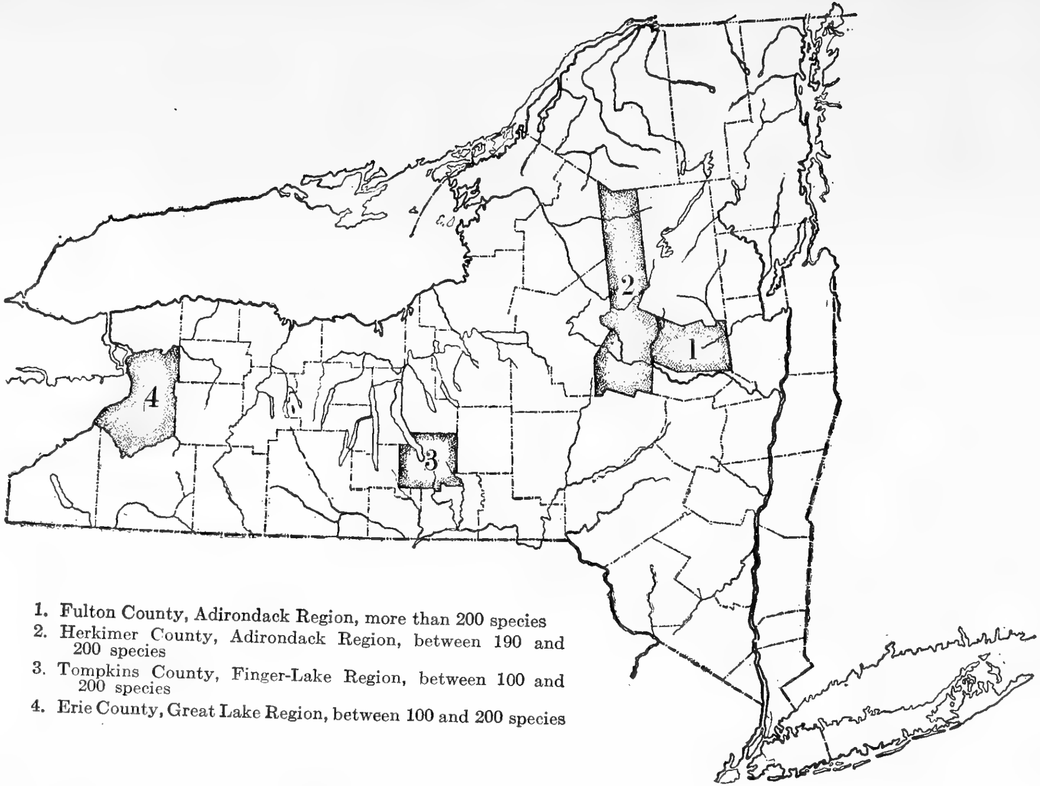
In this list the type localities are designated by the initials *T. L.* The published records of Needham (1908:203–211) and of Alexander (1910 and 1912) have been largely included, altho some of the records for

common and widely distributed species have been omitted. Similarly, many records for Erie, Fulton, and Tompkins Counties have been abbreviated or omitted, since their inclusion would but lengthen the paper and add little to the data; such records are indicated by "etc."

Fulton County, with a known crane-fly fauna of more than two hundred species, probably has the largest local list as known for any region of similar size in the world. The other counties that are well known are Tompkins, Cortland, Herkimer (Osten Sacken, Needham, and Alexander), Albany (Young), and Erie (Van Duzee). Considerable data from Hamilton County (Young), Genesee County (Knight), and Chenango County, are likewise available. The region around New York City is not completely known, the most valuable collections from that section being those made by Frost in Westchester County and by Banks in Nassau County.

The following abbreviations to express collectors are used in this list:

A. C. C.	A. C. Coutant	J. G. N.	J. G. Needham
A. D. M.	A. D. MacGillivray	J. L. Z.	J. L. Zabriskie
A. H. M.	Miss A. H. Morgan	J. S.	J. Silver
A. L. M.	Axel L. Melander	J. T. L.	J. T. Lloyd
A. M.	A. MacDonald	L. W. C.	Mrs. W. A. Clemens
A. M. N.	A. M. Nadler	M. C. VD.	M. C. Van Duzee
A. O.	Axel Olsson	M. D. L.	M. D. Leonard
A. P. M.	A. P. Morse	M. M. A.	Mrs. C. P. Alexander
C. H. K.	C. H. Kennedy	N. B.	Nathan Banks
C. I.	Carl Ilg	O. A. J.	O. A. Johannsen
C. O. H.	C. O. Houghton	O. S.	Osten Sacken
C. P. A.	C. P. Alexander	P. W. C.	P. W. Claassen
C. R. C.	C. R. Crosby	R. C. S.	R. C. Shannon
C. R. P.	C. R. Plunkett	R. F. P.	R. F. Pearsall
D. B. Y.	D. B. Young	R. H. P.	R. H. Pettit
E. M.	Miss E. Moore	R. H. T.	Mrs. J. D. Tothill
E. T. W.	Mrs. W. C. Woods	S. A. G.	S. A. Graham
F. K.	Fritz Kahn	S. C. B.	S. C. Bishop
F. N. H.	F. N. Harvey	S. W. F.	S. W. Frost
H. E. S.	H. E. Schradieck	W. A. C.	W. A. Clemens
H. H. K.	H. H. Knight	W. A. H.	W. A. Hoffman
H. H. S.	H. H. Smith	W. A. R.	W. A. Riley
H. Y.	Hachiro Yuasa	W. D. F.	W. D. Funkhouser
J. A. L.	J. A. Lintner	W. P. A.	W. P. Alexander
J. C. B.	J. Chester Bradley	W. S.	W. Sheffield
J. C. F.	J. C. Faure	W. T. M. F.	W. T. M. Forbes



1. Fulton County, Adirondack Region, more than 200 species
2. Herkimer County, Adirondack Region, between 190 and 200 species
3. Tompkins County, Finger-Lake Region, between 100 and 200 species
4. Erie County, Great Lake Region, between 100 and 200 species

FIG. 121. COUNTIES IN NEW YORK STATE IN WHICH CONSIDERABLE COLLECTIONS OF CRANE-FLIES HAVE BEEN MADE

Family **Tanyderidae**

Genus *Protoplasa* Osten Sacken
Protoplasa fitchii O. S.
Fulton County: Sport Island, Sacandaga River, altitude 750 feet, June 6–19 (C. P. A.).
(Fitch's type locality is New York State.)

Family **Ptychopteridae**

Subfamily **Ptychopterinae**

Genus *Ptychoptera* Meigen
Ptychoptera rufocincta O. S.
Chautauqua County: Dunkirk, July 5.
Dutchess County: Poughkeepsie, May 24 (D. B. Y.).
Erie County: Hamburg, June 6 to July 10 (M. C. VD.); Colden, June 7 (M. C. VD.); East Aurora, June 11 to August 21 (M. C. VD.); etc.
Fulton County: Sacandaga Park, June 11 to August 24 (C. P. A.).
Genesee County: Batavia, June 19 (H. H. K.).
Nassau County: Sea Cliff (N. B.).
Onondaga County: Manlius, August 29 (H. H. S.).
Suffolk County: Yaphank, May 20.
Tompkins County: Ithaca, May 31 to July 5 (C. P. A.).
Westchester County: Dobbs Ferry (O. S.), T. L.
Wyoming County: Portage Falls, July 27 (H. H. K.).

Subfamily **Bittacomorphinae**

Genus *Bittacomorpha* Westwood
Bittacomorpha clavipes (Fabr.)
Cattaraugus County: Little Valley, August 7 (M. C. VD.).
Cayuga County: North Fair Haven, May 17 (E. M. and J. G. N.).
Chenango County: Lower Cincinnatus, July 21 (C. P. A.).
Cortland County: Taylor, July 20 (C. P. A.).
Dutchess County: Poughkeepsie, July 18 (S. W. F.).
Erie County: Colden, May 23-30 (M. C. VD.); Hamburg, June 6 (M. C. VD.); etc.
Fulton County: Sacandaga Park, etc., June 13 to September 13 (C. P. A.).
Herkimer County: Indian Castle, June 9 (C. P. A.); Old Forge, August 21 (J. G. N.).
Nassau County: Sea Cliff (N. B.).
Oneida County: McMullen's Brook, May 20 (W. A. C.).
Onondaga County: Manlius, September 23 (H. H. S.).
Suffolk County: Yaphank, May 29–30; Bellport, August 9.
Tompkins County: Ithaca, May 20 to September 28 (C. P. A.); etc.
Warren County: Paradise Bay, Lake George, August 24.

Genus *Bittacomorphella* Alexander
Bittacomorphella jonesi (Johns.)
Albany County: Karner, June 19 (D. B. Y.).
Cortland County: Taylor, July 20 (C. P. A.).
Erie County: South Wales, July 9 (M. C. VD.).
Fulton County: Sacandaga Park, June 11–28 (C. P. A.); Mountain Lake, June 13–24 (C. P. A.); etc.
Tompkins County: Ithaca, Bool's, July 13–19 (C. P. A.).

Family **Rhyphidae**

Subfamily **Trichocerinae**

Genus *Trichocera* Meigen
Subgenus *Trichocera* Meigen
Trichocera bimacula Walk.
Erie County: Gowanda, October 4 (M. C. VD.); East Aurora, October 20 (M. C. VD.).
Fulton County: Gloversville, September 15 (C. P. A.); etc.
Tompkins County: Ithaca, May 20, October 15 (C. P. A.); etc.
T. brumalis Fitch
Fulton County: Gloversville, September 25 to October 15 (C. P. A.); etc.
Tompkins County: Ithaca, September 30 to October 30 (C. P. A.); etc.
Subgenus *Diazosma* Bergroth
Trichocera subsinuata Alex.
Fulton County: Woodworth's Lake, altitude 1650 feet, June 15 (C. P. A.), T. L.

Subfamily **Rhyphinae**

Genus *Rhyphus* Latreille
Rhyphus alternatus Say
Albany County: Albany.
Erie County: East Aurora, May.
Franklin County: Axton, June.
Tompkins County: Ithaca, May to June (O. A. J.).
R. fenestralis (Scop.)
Erie County: Hamburg, April.
Oneida County: New Hartford, April.
Tompkins County: Ithaca, April to May (O. A. J.).
R. punctatus (Fabr.)
Erie County.
Fulton County: Johnstown.
Tompkins County: Ithaca, May to October (O. A. J.).

Subfamily **Mycetobiinae**

Genus *Mycetobia* Meigen
Mycetobia divergens Walk.
Albany County: Albany.
Tompkins County: Ithaca, May (O. A. J.).

Family **Tipulidae**

Subfamily **Limnobiinae**

Tribe **Limnobiini**

Genus *Dicranomyia* Stephens
Dicranomyia badia (Walk.)
Cortland County: Taylor, July 20 (C. P. A.).
Erie County: Holland, May 21 (M. C. VD.); Boston, July 10 (M. C. VD.); East Aurora, September 20 (M. C. VD.); etc.
Fulton County: Gloversville, June 3 (C. P. A.); Sacandaga Park, June 5 (C. P. A.); etc.

Genus *Dicranomyia* Stephens (*continued*)

Dicranomyia badia (Walk) (*continued*)

Hamilton County: Augur Flats, July 17 (D. B. Y.); Wells, July 29 (D. B. Y.).
Herkimer County: Trenton Falls (O. S.).
Nassau County: Sea Cliff, April (N. B.).
Niagara County: Niagara Falls, October 9 (M. C. VD.).
Schoharie County: Sharon Springs (O. S.).
Tompkins County: Ithaca, May 4 to November 10 (C. P. A.); etc.

D. brevivena O. S.

Cayuga County: North Fair Haven, September 12 (C. P. A.).
Erie County: Lancaster, June 22 (M. C. VD.); Buffalo, September 30 (M. C. VD.).
Fulton County: Sulphur Spring Junction, September (C. P. A.).
Herkimer County: Indian Castle, June 9 (C. P. A.).
New York: (O. S.), T. L.
Niagara County: Niagara Falls, October 9 (M. C. VD.).

D. gladiator O. S.

Fulton County: Woodworth's Lake, August 22 (C. P. A.).

D. globithorax O. S.

Erie County: Boston, September 3 (M. C. VD.).
Fulton County: Woodworth's Lake, August 4–22 (C. P. A.); etc.
Tompkins County: Ellis Hollow, May 14 (C. P. A.); Ithaca, September 28 (J. G. N.).

D. haeretica O. S.

Erie County: Buffalo, October 14 (M. C. VD.).
New York: On salt marshes near New York (O. S.), T. L.
Suffolk County: Cold Spring Harbor, July 15 (A. L. M.); Bellport, August 19 (C. P. A.).

D. halterata O. S.

Fulton County: Johnstown, September 15 (C. P. A.); Mud Lake, September 18 (C. P. A.).

D. immodesta O. S.

Cayuga County: North Fair Haven, September 12 (C. P. A.).
Cortland County: Taylor, July 20 (C. P. A.)
Erie County: Buffalo, October 3–15 (M. C. VD.).
Fulton County: Gloversville, June 9 (C. P. A.); Johnstown, September 15 (C. P. A.); etc.
Herkimer County: Trenton Falls (O. S.), T. L.; Indian Castle, June 9–13 (C. P. A.); Old Forge, August (J. G. N.).
Tompkins County: Ithaca, June 20 (C. P. A.); McLean, September 28 (C. P. A.); etc.

D. liberta O. S.

Albany County: Karner, May 22 (D. B. Y.); Albany, June 2–19 (D. B. Y.).
Cortland County: Taylor, July 20 (C. P. A.).
Erie County: Holland, May 21 (M. C. VD.); Hamburg, May 28 to September 11 (M. C. VD.); Lancaster, June 4 to August 14 (M. C. VD.); Buffalo, June 12 to August 25 (M. C. VD.); etc.
Fulton County: Gloversville, June 10 to September 20 (C. P. A.); etc.
Herkimer County: Indian Castle, June 9 (C. P. A.).
Nassau County: Sea Cliff (N. B.).
New York: (O. S.), T. L.
Onondaga County: Green Lake, June 8 (C. P. A.).
Suffolk County: Bellport, July 1.
Tompkins County: Ithaca, May 22 to June 20 (C. P. A.); etc.
Westchester County: Tarrytown, June 25 (S. W. F.).

Genus *Dicranomyia* Stephens (*continued*)

D. longipennis (Schum.)

Erie County: Hamburg, September 11 (M. C. VD.).
Fulton County: Hillside Park, August 4 (C. P. A.); Sacandaga Park, August 24 (C. P. A.); etc.
Herkimer County: Trenton Falls (O. S.).
Nassau County: Sea Cliff (N. B.).
Rockland County: West Nyack, June 15 (W. S.).
Tompkins County: Ithaca, June 20 to August 1 (C. P. A.); McLean, September 28 (C. R. C.).

D. macateei Alex.

Fulton County: Sylvan Lake, June 15 (C. P. A.); Mountain Lake, July 7 (C. P. A.).

D. moniliformis Doane

Suffolk County: Long Island, T. L.

D. monticola (Alex.)

Chenango County: Lower Cincinnatus, July 21 (C. P. A.).
Cortland County: Taylor, July 20 (C. P. A.).
Fulton County: Gloversville, June 24 (C. P. A.).
Hamilton County: Wells, July 23–30 (D. B. Y.).
Tompkins County: Ithaca, reared June 3 (C. P. A.).

D. morioides O. S.

Erie County: Hamburg, May 3 (M. C. VD.).
Fulton County: Mayfield Mountain, June 21 (C. P. A.); Northampton, June 25 (D. B. Y.); etc.
Herkimer County: Indian Castle, June 9 (C. P. A.); Trenton Falls, July (O. S.), T. L.
Tompkins County: McLean, May 13 (C. P. A.); Ithaca, May 18 to August 26 (C. P. A.).

D. pubipennis O. S.

Chenango County: Lower Cincinnatus, July 21 (C. P. A.).
Cortland County: Taylor, July 20 (C. P. A.).
Erie County: Holland, May 21 (M. C. VD.); Buffalo, June 9 (M. C. VD.); Boston, September 3 (M. C. VD.); etc.
Fulton County: Mountain Lake, June 17 to July 7 (C. P. A.); Gloversville, September 16 (C. P. A.); etc.
Hamilton County: Wells, July 7–25 (D. B. Y.).
Nassau County: Sea Cliff, June (N. B.).
Tompkins County: Ithaca, August 1 (C. P. A.); etc.
Westchester County: Tarrytown, June 9–16 (S. W. F.).

D. pudica O. S.

Chenango County: Lower Cincinnatus, July 21 (C. P. A.).
Cortland County: Taylor, July 20 (C. P. A.).
Erie County: North Evans, May 14 (M. C. VD.); East Aurora, May 18 (M. C VD.); Lancaster, May 31 (M. C. VD.); Boston, July 10 (M C. VD.); etc.
Fulton County: Sylvan Lake, June 15 (C. P. A.).
Schenectady County: Schenectady, June 14 (C. P. A.).
Tompkins County: Ithaca, June.

D. rara O. S.

Genesee County: Batavia, September 28 (H. H. K.).
New York: (O. S.), T. L.
Westchester County: Tarrytown, June 9 (S. W. F.).

D. rostrifera O. S.

Cayuga County: North Fair Haven, September 12 (C. P. A.).

Genus *Dicranomyia* Stephens (*continued*)

D. rostrifera O. S. (*continued*)

Fulton County: Sacandaga Park, June 27 to August 28 (C. P. A.); Sammonsville, September 22 (C. P. A.); etc.

New York: (O. S.), T. L.

D. simulans (Walk.)

Albany County: Helderbergs, July 3 (C. P. A.).

Cortland County: Taylor, July 20 (C. P. A.).

Erie County: Lancaster, June 23 (M. C. VD.); South Wales, June 23 to July 9 (M. C. VD.); etc.

Fulton County: Dolgeville, May 16 (C. P. A.).

Herkimer County: Trenton Falls (O. S.); Old Forge, July 16 (J. G. N.).

Nassau County: Sea Cliff, July (N. B.).

Oneida County: Tannery Brook, July 12 (W. A. C.).

Tompkins County: Ithaca, May 30 to November 14 (C. P. A.); etc.

Westchester County: Tarrytown, August 1 (S. W. F.).

D. stulta O. S.

Fulton County: Mountain Lake, June 14 (C. P. A.).

Herkimer County: Trenton Falls (O. S.), T. L.

Tompkins County: Ithaca, reared from larvae, June 1 (C. P. A.); abundant along Cascadilla Creek, June 13–18 (C. P. A.).

Genus *Geranomyia* Haliday

Geranomyia canadensis (Westw.)

Erie County: Lancaster, June 8 to August 15 (M. C. VD.); East Aurora, August 24 (M. C. VD.); Hamburg, September 11 (M. C. VD.); etc.

Fulton County: Canada Lake, June 23 (C. P. A.).

Herkimer County: Indian Castle, June 13 (C. P. A.); Old Forge, August (J. G. N.).

Onondaga County: Manlius, August 20 (H. H. S.).

Tompkins County: Ithaca, May 7 to October 13 (C. P. A.).

G. diversa O. S.

Erie County: Springville, August 12 (M. C. VD.).

Herkimer County: Trenton Falls (O. S.), T. L.

Tompkins County: Ithaca, May 12 to August 26 (C. P. A.).

G. rostrata (Say)

Cayuga County: North Fair Haven, September 12 (C. P. A.).

Erie County: Holland, May 21 (M. C. VD.); Colden, May 30 to August 9 (M. C. VD.); Gowanda, August 22 (M. C. VD.); etc.

Fulton County: Mount Buell, June 15 (C. P. A.); Sacandaga Park, August 24 (C. P. A.).

New York: (O. S.).

Tompkins County: Ithaca, August 27 (A. C. C.).

Genus *Rhipidia* Meigen

Subgenus *Rhipidia* Meigen

Rhipidia bryanti Johns.

Erie County: East Aurora, June 15 (M. C. VD.).

R. maculata Meig.

Chenango County: Lower Cincinnatus, July 21 (C. P. A.).

Cortland County: Taylor, July 20 (C. P. A.).

Essex County: Wilmington, August 24 (J. C. B.).

Fulton County: Woodworth's Lake, September 2 (C. P. A.); etc.

Herkimer County: Trenton Falls (O. S.); Old Forge, July 6–20 (J. G. N.).

Tompkins County: McLean, June 5 (C. P. A.).

Genus *Rhipidia* Meigen (*continued*)

Subgenus *Monorhipidia* Alexander

Rhipidia fidelis O. S.

Albany County: Albany, July 1 (D. B. Y.).
Cortland County: Cincinnatus, July 21 (C. P. A.).
Erie County: Gowanda, June 15 (M. C. VD.).
Fulton County: Sacandaga Park, June 15–27 (C. P. A.); etc.
Schoharie County: Sharon Springs (O. S.), T. L.
Tompkins County: Ithaca, May 15 (C. I.); McLean, June 5 (C. P. A.).

Genus *Limnobia* Meigen

Limnobia cinctipes Say

Cattaraugus County: Little Valley, June 30 (M. C. VD.).
Chenango County: Lower Cincinnatus, July 21 (C. P. A.).
Erie County: East Aurora, May 7 (M. C. VD.).
Essex County: New Russia, August (J. C. B.); Keene Valley, August 14 (J. A. L.).
Fulton County: Dolgeville, May 16 (A. O.); Mount Buell, June 13 (C. P. A.); etc.
Hamilton County: Saranac Inn, June 17 (J. G. N.); Augur Flats, July 17 (D. B. Y.).
Herkimer County: Old Forge, July 29 (J. G. N.).
Onondaga County: Green Lake, June 8 (C. P. A.).
Tompkins County: Ithaca, May 4 (C. P. A.).
Warren County: Lake George, August 29 (J. L. Z.).

L. fallax Johns.

Genesee County: Batavia, May 22 (H. H. K.).
Tompkins County: Ithaca, reared July 21 (O. A. J.).

L. immatura O. S.

Albany County: Albany, June 4 (D. B. Y.).
Erie County: South Wales, July 9 (M. C. VD.).
Fulton County: Sacandaga Park, June 18 (C. P. A.).
Herkimer County: Old Forge, June 17 (J. G. N.).
Tompkins County: McLean, July 27 (H. H. K.).

L. indigena O. S.

Cattaraugus County: Rock City, June 6 (J. C. B.); Little Valley, June 30 (M. C. VD.).
Erie County: Gowanda, June 27 (M. C. VD.); North Evans, July 4 to October 22 (M. C. VD.); etc.
Fulton County: Sacandaga Park, June 13 (C. P. A.); Mayfield Mountain, September 20 (C. P. A.); etc.
Hamilton County: Mount Buell, June 13 (C. P. A.).
Herkimer County: Old Forge, June 17 to August (J. G. N.).
New York: (O. S.), T. L.
Niagara County: Niagara Falls, June 9 (M. C. VD.).
Onondaga County: Manlius, September 1 (H. H. S.).
Saratoga County: Corinth, June 22 (D. B. Y.).
Tompkins County: Ithaca, May 24–29 (C. P. A.); etc.
Westchester County: Tarrytown, June 9 (S. W. F.).

L. parietina O. S.

Erie County: Boston, September 3 (M. C. VD.).
Fulton County: Woodworth's Lake, August 20 (C. P. A.).
Hamilton County: Silver Lake, September 2 (C. P. A.); Big Notch Mountain, Hope Township, September 12 (C. P. A.).
Herkimer County: Old Forge, August 15 (J. G. N.); Trenton Falls, September (O. S.), T. L.
Tompkins County: Needham's Glen, Ithaca, September 17 (J. G. N.).

Genus *Limnobia* Meigen (*continued*)

L. solitaria O. S.

Erie County: (M. C. Van Duzee records *L. hudsonica* from Spring Brook, June 26, 1911. In the absence of specimens this record should be questioned, inasmuch as this is a variable species and close to *solitaria*.)

Essex County: Keene Valley, July 17 (J. A. L.).

Fulton County: Gloversville, June 9 (C. P. A.); Pinnacle Mountain, August 5 (C. P. A.).

Herkimer County: Trenton Falls (O. S.), T. L.; Indian Castle, June 9 (C. P. A.).

Tompkins County: Ithaca, May 6 to June 20 (C. P. A.).

Ulster County: Catskills, July (O. S.).

L. triocellata O. S.

Cortland County: Taylor, July 20 (C. P. A.).

Erie County: Gowanda, June 13–14 (M. C. VD.); Hamburg, August 10 (M. C. VD.); etc.

Fulton County: Woodworth's Lake, August 22 (C. P. A.); etc.

Hamilton County: Elm Lake, August 7 (D. B. Y.).

Herkimer County: Trenton Falls (O. S.), T. L.

Onondaga County: Manlius, September 1 (H. H. S.).

Putnam County: Highlands, October 3 (J. S.).

Rockland County: West Nyack, June 15 (W. S.).

Tompkins County: Ithaca, August 25 (W. D. F.).

L. tristigma O. S.

Chenango County: Lower Cincinnatus, July 21 (C. P. A.).

Cortland County: Taylor, July 20 (C. P. A.).

Essex County: Elizabethtown, August 12 (D. B. Y.).

Fulton County: Gloversville, July 3 (C. P. A.); Woodworth's Lake, August 24 (C. P. A.); etc.

Hamilton County: Dug Mountain, August 8 (D. B. Y.).

Herkimer County: Old Forge, August 15 (J. G. N.).

Niagara County: Niagara Falls, July 20 (M. C. VD.).

Rensselaer County: Brookview, July 13 (M. M. A.).

Warren County: County-Line Flow, Griffin, July 26 (C. P. A.).

Genus *Discobola* Osten Sacken

Discobola argus (Say)

Albany County: Karner, October 17 (D. B. Y.).

Cattaraugus County: Little Valley, July 31 (M. C. VD.).

Chenango County: Near Lower Cincinnatus, July 21 (C. P. A.).

Erie County: East Aurora, June 11–22 (M. C. VD.); Gowanda, October 4 (M. C. VD.); Hamburg, October 16 (M. C. VD.); etc.

Essex County: New Russia, August (J. C. B.); Mount Whiteface, altitude 4800 feet, August 24 (C. R. C. and W. T. M. F.).

Fulton County: Green Lake, June 25 (C. P. A.); Gloversville, September 20 (C. P. A.); etc.

Genesee County: Batavia, June 18 (H. H. K.).

Hamilton County: Saranac Inn, July 30 (J. G. N.); Wells, August 3 (D. B. Y.).

Herkimer County: Trenton Falls (O. S.); Old Forge, August 23 (J. G. N.).

Monroe County: Rochester, October 10 (M. C. VD.).

Nassau County: Sea Cliff, May (N. B.).

Tompkins County: Ithaca, August 7 to October 3 (C. I.); etc.

Yates County: Keuka Park, October 29 (C. R. C.).

nal species: *Dicranomyia brunnea* Doane, *D. diversa* O. S., *D. isabellina* Doane, *Jeranomyia distincta* Doane, *Limnobia sociabilis* O. S., *Rhipidia domestica* O. S.. *R hannoni* Alex.

Antochini

s *Rhamphidia* Meigen
Rhamphidia flavipes Macq.
Albany County: Albany, July 19 (D. B. Y.).
Erie County: Buffalo, May 28 (M. C. VD.).
Fulton County: Sacandaga Park, June 2 to August 24 (C. P. A.); etc.
New York: (O. S.).
Queens County: Flushing, June 22 (C. R. P.).
Tompkins County: Ithaca, May 29 to August 7 (C. P. A.); etc.
?. mainensis Alex.
Tompkins County: Larch Meadows, Ithaca, reared May 14 (C. P. A.).

s *Elephantomyia* Osten Sacken
Elephantomyia westwoodi O. S.
Cortland County: Lower Cincinnatus, July 21 (C. P. A.).
Erie County: South Wales, July 9 (M. C. VD.); Hamburg, July 10 (M. C. VD.); Springville, July 12 (M. C. VD.).
Fulton County: Mountain Lake, June 24 to August 13 (C. P. A.); etc.
Hamilton County: Wells, July 30 (D. B. Y.).
Herkimer County: Trenton Falls (O. S.), T. L.; Old Forge, August 3 (J. G. N.).
Ulster County: Catskills, July, 1874 (O. S.).

Toxorhina Loew
oxorhina muliebris (O. S.)
Erie County: Hamburg, July 10 (M. C. VD.).
Fulton County: Sacandaga Park, June 21–28 (C. P. A.).
Suffolk County: Yaphank, June 28 (A. M. N.).
Tompkins County: Ithaca (R. H. T.); McLean, July 3 (A. D. M.).

Dicranoptycha Osten Sacken
icranoptycha germana O. S.
Chenango County: Lower Cincinnatus, July 21 (C. P. A.).
Cortland County: Taylor, July 20 (C. P. A.).
Erie County: South Wales, July 9 (M. C. VD.).
Fulton County: Sacandaga Park, June 21–28 (C. P. A.).
Hamilton County: Augur Flats, July 17 (D. B. Y.); Wells, July 30 (D. B. Y.).
Herkimer County: Trenton Falls, July (O. S.), T. L.; Old Forge, July 6–24 (J. G. N.).
Onondaga County: Manlius, July 25 (H. H. S.).
Tompkins County: Ithaca, July 13 (C. P. A.).
Warren County: County-Line Flow, Griffin, July 26 (C. P. A.).
sobrina O. S.
Cayuga County: North Fair Haven, September 12 (C. P. A.).
Fulton County: Mayfield Mountain, September 20 (C. P. A.).
Tompkins County: Ithaca, August 30 (J. G. N.).

Antocha Osten Sacken
ntocha saxicola O. S.
Cortland County: Taylor, July 20 (C. P. A.).
Erie County: Lancaster, June 2 (M. C. VD.); Buffalo, June 15 (M. C. VD.).
Fulton County: Sacandaga Park, June 11 to July 3 (C. P. A.); etc.

Genus *Antocha* Osten Sacken (*continued*)

Antocha saxicola O. S. (*continued*)

Herkimer County: Trenton Falls (O. S.), T. L.; Indian Castle, June 9 (C. P
Newport, June 9 to July 27 (D. B. Y.); Old Forge, Ju
(J. G. N.).

Monroe County: Honeoye Falls, May 15 (M. D. L.); September 1 (C. R. C.

Oneida County: Tannery Brook, July 12 (W. A. C.).

Onondaga County: Manlius, August 20 (H. H. S.).

Rensselaer County: Brookview, July 16 (M. M. A.).

Tioga County: Willseyville, May 25 (W. A. H.).

Tompkins County: Ithaca, May 13 to September 25 (C. P. A.); McLean, J
(C. P. A.).

Westchester County: Tarrytown, June 9 (S. W. F.).

Wyoming County: Portage, May 24 (H. H. K.).

Genus *Atarba* Osten Sacken

Atarba picticornis O. S.

Cortland County: Taylor, July 20 (C. P. A.).

Erie County: South Wales, July 9–13 (M. C. VD.).

Fulton County: Sacandaga Park, June 28 (C. P. A.).

Herkimer County: Trenton Falls, July (O. S.).

Suffolk County: Bellport, July 5.

Genus *Teucholabis* Osten Sacken

Teucholabis complexa O. S.

Herkimer County: Trenton Falls, June (O. S.), T. L.

Regional species: *Dicranoptycha nigripes* O. S., *D. winnemana* Alex., *Teucholabis*
Alex., *Toxorhina magna* (O. S.).

Tribe **Eriopterini**

Genus *Ormosia* Rondani

Ormosia apicalis Alex.

Fulton County: Mountain Lake, June 17 (C. P. A.).

Tompkins County: Ithaca, August 8 (J. G. N.).

O. arcuata (Doane)

Erie County: Hamburg, May 7 (M. C. VD.).

Tompkins County: Ithaca, T. L.

O. bilineata Dietz

Erie County: Holland, May 21–25 (M. C. VD.), T. L.

O. deviata Dietz

Cayuga County: North Fair Haven, September 12 (C. P. A.).

Erie County: Hamburg, May 26 (M. C. VD.), T. L.

Fulton County: Mountain Lake, June 1–18 (C. P. A.).

Herkimer County: Indian Castle, June 9 (C. P. A.).

Onondaga County: Green Lake, June 8 (C. P. A.).

Tompkins County: McLean, June 5 (C. P. A.).

Westchester County: Tarrytown, June 9 (S. W. F.).

O. holotricha (O. S.).

Fulton County: Johnstown, May 14 (C. P. A.).

Tompkins County: Ithaca, April 27 to May 22 (C. P. A.); Taughannock,
(C. P. A.).

O. innocens (O. S.).

Albany County: Albany, May 8 (D. B. Y.).

Erie County: Hamburg, May 28 (M. C. VD.).

nus *Ormosia* Rondani (*continued*)

O. innocens (O. S.) (*continued*)

Nassau County: Sea Cliff (N. B.).

Tompkins County: Ithaca, April 24 to May 25 (C. P. A.); McLean, May 13 (C. P. A.).

O. megacera Alex.

Fulton County: Gloversville, June 22 (C. P. A.), T. L.

O. meigenii (O. S.)

Erie County: Colden, May 29 (M. C. VD.).

Fulton County: Johnstown, May 14 (C. P. A.); Gloversville, June 3 (C. P. A.); etc.

Tompkins County: Ithaca, April 26 to May 12 (C. P. A.); McLean, May 13 (C. P. A.).

Westchester County: Tarrytown, June 9 (S. W. F.).

O. mesocera Alex.

Essex County: Uphill Creek and Opalescent River, foot of Mount Marcy, July 10 (C. R. C.).

Fulton County: Gloversville, June 22 (C. P. A.), T. L.

O. monticola (O. S.)

Erie County: Colden, August 7 (M. C. VD.).

Fulton County: Pinnacle Mountain, August 5 (C. P. A.); Sacandaga Park, August 24 (C. P. A.).

Hamilton County: Speculator, August 5 (D. B. Y.).

Herkimer County: Old Forge, August (J. G. N.).

Tompkins County: Ithaca, August 26 (C. P. A.).

O. nigripila (O. S.)

Fulton County: Mountain Lake, June 13 (C. P. A.); Pinnacle, August 5 (C. P. A.).

Nassau County: Sea Cliff, May (N. B.).

Onondaga County: Green Lake, June 8 (C. P. A.).

Tompkins County: McLean, May 22 (H. E. S.); Ithaca, May 31 (R. H. T.).

Westchester County: Tarrytown, June 9 (S. W. F.).

O. nimbipennis Alex.

Fulton County: Woodworth's Lake, August 13 (C. P. A.), T. L.

Hamilton County: Wells, July 29 (D. B. Y.).

O. nubila (O. S.)

Albany County: Albany, May 8 (D. B. Y.).

Erie County: Colden, August 7 (M. C. VD.); Boston, September 3 (M. C. VD.); Lancaster, September 24 to October 18 (M. C. VD.); etc.

Fulton County: Johnstown, May 14 (C. P. A.); etc.

Herkimer County: Trenton Falls (O. S.), T. L.

Nassau County: Sea Cliff, May (N. B.).

Tompkins County: Ithaca, April 24 to May 16 (C. P. A.); McLean, May 13 (C. P. A.).

O. parallela (Doane)

Tompkins County: Ithaca, T. L.

O. perplexa Dietz

Erie County: Waverly, May (M. C. VD.), T. L.

O. pygmaea (Alex.)

Erie County: Hamburg, May 28 (M. C. VD.).

Fulton County: Woodworth's Lake, August 22 (C. P. A.), T. L.

Tompkins County: Ithaca, May 28 (W. S.).

O. rubella (O. S.)

Erie County: Colden, August 7 (M. C. VD.); Lancaster, September 24 to October 18 (M. C. VD.); etc.

Genus *Ormosia* Rondani (*continued*)

O. rubella (O. S.) (*continued*)

Fulton County: Mayfield Mountain, September 20 (C. P. A.); etc.
Niagara County: Niagara Falls, September 8 to October 17 (M. C. VD.).
Orange County: West Point (O. S.), T. L.

Genus *Erioptera* Meigen

Subgenus *Erioptera* Meigen

Erioptera chlorophylla O. S.

Albany County: Albany, June 28 (D. B. Y.).
Erie County: Gowanda, June 15 (M. C. VD.); South Wales, July (M. C. VD.); Hamburg, July 27 (M. C. VD.); etc.
Franklin County: Saranac Inn, July 4 (J. G. N.).
Fulton County: Sacandaga Park, June 15 to August 24 (C. P. A.); etc.
Herkimer County: Old Forge, July 29 (J. G. N.).
Queens County: Flushing, June 22 (C. R. P.); Little Ferry, August (C. R. P.).
Tompkins County: Ithaca, July 10–13 (C. P. A.).

E. chrysocoma O. S.

Fulton County: Mountain Lake, June 15 to July 7 (C. P. A.); Sacand Park, June 18 (C. P. A.).
Westchester County: Tarrytown, June 9 (S. W. F.).

E. megophthalma Alex.

Fulton County: Sacandaga Park, June 18 (C. P. A.); etc.
Herkimer County: Indian Castle, June 9–13 (C. P. A.).
Tompkins County: Ithaca, May 28 to June 13 (C. P. A.), T. L.
Westchester County: Tarrytown, June 9 (S. W. F.).

E. septemtrionis O. S.

Erie County: Gowanda, June 7 (M. C. VD.); East Aurora, June (M. C. VD.).
Essex County: Uphill Creek and Opalescent River, foot of Mount Ma July 10 (C. R. C.).
Fulton County: Mount Buell, June 5–18 (C. P. A.); Mountain L August 13 (C. P. A.); etc.
Herkimer County: Old Forge, July 17–21 and in August (J. G. N.).
Madison County: Canastota (J. C. F.).
Oneida County: Lee Center, July 24 (W. A. C.).
Schoharie County: Sharon Springs (O. S.), T. L.
Tompkins County: Ithaca, April 26 to July 13 (C. P. A.); McLean, Ma to June 5 (C. P. A.).

E. straminea O. S.

Erie County: Gowanda, June 14–27 (M. C. VD.); Grand Island, June (M. C. VD.).
Fulton County: Sacandaga Park, June 18 (C. P. A.).

E. vespertina O. S.

Cattaraugus County: Chipmunk Swamp, Vandalia, June 9 (C. R. C.).
Erie County: Hamburg, June 20 (M. C. VD.).
Fulton County: Sacandaga Park, June 5–28 (C. P. A.); etc.
Tompkins County: Ithaca, May 15 to July 13 (C. P. A.); etc.

E. villosa O. S.

Erie County: Holland, May 21 (M. C. VD.); North Evans, May (M. C. VD.); Buffalo, June 23 to July 9 (M. C. V Spring Brook, June 25 (M. C. VD.); Gowanda, June (M. C. VD.).

enus *Erioptera* Meigen (*continued*)

Subgenus *Acyphona* Osten Sacken

Erioptera armillaris O. S.

Chenango County: Near Lower Cincinnatus, July 21 (C. P. A.).
Cortland County: Lower Cincinnatus, July 21 (C. P. A.).
Erie County: South Wales, July 9 (M. C. VD.); Elma, August 24 (M. C. VD.).
Fulton County: Sacandaga Park, June 11–18 (C. P. A.); Mountain Lake, June 17 to July 7 (C. P. A.).
Herkimer County: Trenton Falls (O. S.), T. L.
Tompkins County: McLean, June 5 (C. P. A.); Ithaca, August 30 (C. P. A.).

E. graphica O. S.

Tompkins County: Ithaca, July 13 (H. Y.), August 2–7 (C. P. A.).

E. venusta O. S.

Albany County: Helderbergs, June 12 (C. P. A.); Albany, June 26 to September 20 (D. B. Y.).
Erie County: Gowanda, June 7–27 (M. C. VD.); Hamburg, June 18–20 (M. C. VD.); Colden, August 16 (M. C. VD.); etc.
Fulton County: Gloversville, June 3 to September 20 (C. P. A.); etc.
Genesee County: Batavia, July 25 (H. H. K.).
Herkimer County: Indian Castle, June 9 (C. P. A.); Newport, June 18 (D. B. Y.); Old Forge, August (J. G. N.).
Monroe County: Rochester Junction, June 1 (M. D. L.).
Oneida County: Lee Center, July 26 (W. A. C.).
Queens County: Flushing, June 22 (C. R. P.).
Schenectady County: Schenectady, June 14 (C. P. A.).
Tompkins County: Ithaca, May 23 to August 12 (C. P. A.); etc.
Westchester County: Tarrytown, June 9 (S. W. F.).

Subgenus *Hoplolabis* Osten Sacken

Erioptera armata O. S.

Erie County: Hamburg, May 14 to September 5 (M. C. VD.); East Aurora, May 18 (M. C. VD.); Buffalo, May 22 (M. C. VD.); Lancaster, June 19 to August 14 (M. C. VD.); etc.
Fulton County: Sacandaga Park, June 1 to August 24 (C. P. A.); etc.
Herkimer County: Indian Castle, June 9–13 (C. P. A.).
Monroe County: Rochester Junction, June 1 (M. D. L.).
Tompkins County: Ithaca, May 12–15 (C. P. A.); McLean, September 28 (C. P. A.).
Westchester County: Tarrytown, June 9 (S. W. F.).

Subgenus *Mesocyphona* Osten Sacken

Erioptera caloptera Say

Albany County: Helderbergs, July 3 (C. P. A.).
Cayuga County: North Fair Haven, September 14 (C. P. A.).
Chenango County: Lower Cincinnatus, July 21 (C. P. A.).
Cortland County: Taylor, July 20 (C. P. A.).
Erie County: Gowanda, June 7 (M. C. VD.); Buffalo, June 23–25 (M. C. VD.); East Aurora, August 21 (M. C. VD.); etc.
Fulton County: Sacandaga Park, June 15 to August 24 (C. P. A.); etc.
Herkimer County: Indian Castle, June 9 (C. P. A.).
Queens County: Flushing, June 14 (C. R. P.).
Tompkins County: Ithaca, May 13 to June 19 (C. P. A.); McLean, June 5 (C. P. A.).
Westchester County: Tarrytown, June 9 (S. W. F.).

Genus *Erioptera* Meigen (*continued*)

Subgenus *Mesocyphona* Osten Sacken (*continued*)

E. needhami Alex.

Cortland County: Cincinnatus, July 21 (C. P. A.).
Fulton County: Sacandaga Park, June 11–18 (C. P. A.).
Herkimer County: Indian Castle, June 9 (C. P. A.).
Onondaga County: Green Lake, June 8 (C. P. A.).
Tompkins County: Ithaca (R. H. T.).

E. parva O. S.

Cayuga County: North Fair Haven, September 12 (C. P. A.).
Erie County: Colden, August 7 (M. C. VD.).
Fulton County: Johnstown, September 15 (C. P. A.).
Tompkins County: Ithaca, August 2 (C. P. A.).

Subgenus *Empeda* Osten Sacken

Erioptera nyctops Alex.

Fulton County: Mountain Lake, June 13 (C. P. A.), T. L.; Mount Bu June 18 (C. P. A.).

E. stigmatica (O. S.)

Albany County: Helderbergs, June 12 to July 3 (C. P. A.).
Chenango County: Lower Cincinnatus, July 21 (C. P. A.).
Cortland County: Taylor, July 20 (C. P. A.).
Erie County: Holland, May 21–28 (M. C. VD.); East Aurora, June 1 (M VD.); Lancaster, September 24 (M. C. VD.).
Fulton County: Sacandaga Park, June 5–24 (C. P. A.); etc.
Herkimer County: Trenton Falls (O. S.), T. L.
Tompkins County: Ithaca, May 12 to June 20 (C. P. A.); McLean, Sept ber 28 (H. H. K.).

Genus *Molophilus* Curtis

Molophilus forcipula (O. S.)

Erie County: East Aurora, August 21 (M. C. VD.).
Fulton County: Gloversville, July 16 (C. P. A.).
Niagara County: Niagara Falls, October 9 (M. C. VD.).

M. fultonensis Alex.

Chenango County: Lower Cincinnatus, July 21 (C. P. A.).
Cortland County: Taylor, July 20 (C. P. A.).
Fulton County: Mountain Lake, July 7 (C. P. A.), T. L.

M. hirtipennis (O. S.)

Albany County: Helderbergs, July 3 (C. P. A.).
Erie County: Hamburg, May 28 (M. C. VD.); Gowanda, June 8 (M. C. V Elma, August 20 (M. C. VD.).
Fulton County: Johnstown, June 3–30 (C. P. A.); Mountain Lake, June (C. P. A.).
Herkimer County: Indian Castle, June 9 (C. P. A.); Old Forge, July and Au (J. G. N.).
Oneida County: North Brook, June 22 (W. A. C.).
Onondaga County: Green Lake, June 8 (C. P. A.).
Tompkins County: Ithaca, May 29 to June 18 (C. P. A.); McLean, Ju (C. P. A.).
Westchester County: Tarrytown, June 9 (S. W. F.).

M. pubipennis (O. S.)

Chenango County: Lower Cincinnatus, July 21 (C. P. A.).
Cortland County: Taylor, July 20 (C. P. A.).
Erie County: Lancaster, June 19 (M. C. VD.); South Wales, July 9 (M. C. V

us *Molophilus* Curtis (*continued*)
M. pubipennis (O. S.) (*continued*)
Essex County: Uphill Creek and Opalescent River, foot of Mount Marcy, July 10 (C. R. C.).
Fulton County: Sacandaga Park, June 3 to August 11 (C. P. A.); etc.
Hamilton County: Wells, July 7–29 (D. B. Y.).
Herkimer County: Indian Castle, June 13 (C. P. A.); Old Forge, August (J. G. N.).
Oneida County: Potash Creek, July 24 (W. A. C.).
Onondaga County: Green Lake, June 8 (C. P. A.).
Tompkins County: Ithaca, May 29 to July 13 (C. P. A.); etc.
Westchester County: Tarrytown, June 9 (S. W. F.).
M. ursinus (O. S.)
Chenango County: Lower Cincinnatus, July 21 (C. P. A.).
Fulton County: Mayfield Mountain, June 21 to July 7 (C. P. A.); etc.
Herkimer County: Indian Castle, June 13 (C. P. A.).

us *Trimicra* Osten Sacken
Trimicra anomala O. S.
Erie County: Hamburg, May 28 (M. C. VD.); South Wales, July 9 (M. C. VD.).
Westchester County: New Rochelle (O. S.), T. L.

us *Helobia* St. Fargeau et Serville
Helobia hybrida (Meig.)
Albany County: Clinton Heights, April 9 (D. B. Y.); Karner, June 5 (D. B. Y.).
Erie County: Buffalo, March 4 to October 3 (M. C. VD.); Lancaster, May 9 (M. C. VD.); etc.
Fulton County: Johnstown, June 30 (C. P. A.); etc.
Hamilton County: Elm Lake, August 7 (D. B. Y.).
Herkimer County: Newport, June 18 (D. B. Y.); Old Forge, July 20–24 (J. G. N.).
Madison County: Canastota (J. C. F.).
Queens County: Flushing, June 22 (C. R. P.).
Tompkins County: Ithaca, March 25 to August 7 (C. P. A.); etc.

us *Gnophomyia* Osten Sacken
Gnophomyia tristissima O. S.
Albany County: Albany, September 11 (D. B. Y.).
Dutchess County: Poughkeepsie, June 8 (D. B. Y.).
Erie County: Gowanda, June 15 (M. C. VD.); Buffalo, June 25 to August 25 (M. C. VD.); etc.
Fulton County: Sacandaga Park, June 6 to August 24 (C. P. A.); Johnstown, September 20 (C. P. A.); etc.
Nassau County: Sea Cliff, September 3–5 (N. B.).
Niagara County: Niagara Falls, July 30 to October 9 (M. C. VD.).
Rensselaer County: Rensselaer, June 3 (D. B. Y.).
Suffolk County: O. S., in the type series at Cambridge.
Tompkins County: Ithaca, May 30 to June 10 (J. G. N.); Norton's Landing, June 19 (H. H. S.); etc.
Westchester County: Tarrytown, June 16–25 (S. W. F.).

s *Gonomyia* Meigen
ubgenus *Leiponeura* Skuse
Gonomyia alexanderi (Johns.)
Fulton County: Sacandaga Park, June 11 to August 24 (C. P. A.), T. L.
Herkimer County: Indian Castle, June 13 (C. P. A.).
G. manca (O. S.)
Fulton County: Sacandaga Park, August 26 (C. P. A.).

Genus *Gonomyia* Meigen (*continued*)
Subgenus *Leiponeura* Skuse (*continued*)
G. sacandaga Alex.
Fulton County: Sacandaga Park, June 11 to August 24 (C. P. A.), T. L.
Subgenus *Gonomyia* Meigen
Gonomyia blanda O. S.
Albany County: Albany, June 26 (D. B. Y.).
Cortland County: Taylor, July 20 (C. P. A.).
Herkimer County: Trenton Falls (O. S.), T. L.
Tompkins County: Ithaca, July 19 (C. P. A.).
G. cognatella O. S.
Erie County: Gowanda, June 8 (M. C. VD.).
Fulton County: Sacandaga Park, June 18 to August 26 (C. P. A.).
Herkimer County: Indian Castle, June 10–13 (C. P. A.).
G. florens Alex.
Fulton County: Sacandaga Park, June 18 (C. P. A.); Gloversville, June (C. P. A.).
Herkimer County: Indian Castle, June 9–13 (C. P. A.), T. L.
Tompkins County: McLean, June 5 (C. P. A.).
G. mathesoni Alex.
Cortland County: Taylor, July 20 (C. P. A.).
Fulton County: Sacandaga Park, June 12–16 (C. P. A.), T. L.
Herkimer County: Indian Castle, June 13 (C. P. A.).
Tompkins County: Ithaca, August 24 (C. P. A.).
G. noveboracensis Alex.
Fulton County: Sacandaga Park, June 11 (C. P. A.), T. L.
G. subcinerea O. S.
Albany County: Helderbergs, June 12 (C. P. A.); Albany, June 26 (D. B. Y
Erie County: Lancaster, June 4 (M. C. VD.); Hamburg, July 10 (M. C. VD etc.
Fulton County: Sacandaga Park, June 1 (C. P. A.); Gloversville, June (C. P. A.); etc.
Herkimer County: Trenton Falls (O. S.), T. L.; Indian Castle, June 9- (C. P. A.).
Onondaga County: Green Lake, June 8 (C. P. A.).
Rensselaer County: Brookview, July 13 (M. M. A.).
Rockland County: West Nyack, June 15 (W. S.).
Tompkins County: Ithaca, May 13 to August 7 (C. P. A.).
Westchester County: Tarrytown, June 9 (S. W. F.).
G. sulphurella O. S.
Clinton County: Peru, June 10 (C. R. C.).
Erie County: Lancaster, June 2 to August 14 (M. C. VD.); Buffalo, June (M. C. VD.); Elma, August 27 (M. C. VD.); etc.
Fulton County: Sacandaga Park, June 11 to August 24 (C. P. A.); etc.
Herkimer County: Trenton Falls (O. S.), T. L.; Indian Castle, June 13 (C. P. A
Nassau County: Sea Cliff, August (N. B.).
Tompkins County: Ithaca, May 13 to August 24 (C. P. A.).
Westchester County: Tarrytown, June 9 (S. W. F.).

Genus *Rhabdomastix* Skuse
Subgenus *Sacandaga* Alexander
Rhabdomastix flava (Alex.)
Fulton County: Sacandaga Park, June 11–28 (C. P. A.), T. L.
Hamilton County: Wells, July 6 (D. B. Y.).
Herkimer County: Indian Castle, June 13 (C. P. A.).

Genus *Cryptolabis* Osten Sacken

Cryptolabis paradoxa O. S.

Cortland County: Taylor, July 20 (C. P. A.).
Fulton County: Sacandaga Park, June 18 to July 27 (C. P. A.).
Oneida County: Brown Brook, July 13 (W. A. C.).
Tompkins County: Ithaca, June 19–21 (C. P. A.); Enfield Falls, July 12.

Genus *Cladura* Osten Sacken

Cladura delicatula Alex.

Fulton County: Mayfield Mountain, October 1 (C. P. A.).
Hamilton County: Middle Lake, Hope Township, September 12–13 (C. P. A.).

C. flavoferruginea O. S.

Erie County: East Aurora, September 20 (M. C. VD.); Lancaster, September 24 (M. C. VD.); Hamburg, September 25 to October 16 (M. C. VD.); North Evans, October 22 to November 4 (M. C. VD.); etc.
Fulton County: Pinnacle Mountain, August 5 (C. P. A.); Mayfield Mountain, September 20 (C. P. A.).
Genesee County: Batavia, September 28 (H. H. K.).
Hamilton County: Middle Lake, Hope Township, September 12 (C. P. A.).
Herkimer County: Trenton Falls, September (O. S.), T. L.
Monroe County: Rochester, October 10 (M. C. VD.).
Nassau County: Sea Cliff (N. B.).
Niagara County: Niagara Falls, October 9 (M. C. VD.).
Onondaga County: Manlius, October 1 (H. H. S.).
Putnam County: Highlands, October 3 (J. S.).
Tioga County: Owego, October 24 (H. H. K.).
Tompkins County: McLean, September 28 (C. R. C. and H. H. K.); Ithaca, October 3–15 (C. P. A.).

Genus *Chionea* Dalman

Chionea gracilis Alex.

Tompkins County: Ithaca, December 15, T. L.

C. noveboracensis Alex.

Tompkins County: Ithaca, Coy Glen, February 25 (R. C. S.), T. L.

C. primitiva Alex.

Cayuga County: Cascade, Owasco Lake, November 15 (S. C. B. and C. R. C.), T. L.

C. valga Harris

Cattaraugus County: Otto, March 18.
Erie County: Lancaster (M. C. VD.), on snow.
Onondaga County: Manlius, October 1 (H. H. S.).
Steuben County: Lake Keuka, December (C. R. C.).
Tompkins County: Ithaca, November 18 (R. H. P.); December 15 (W. A. R.).

Regional species: *Molophilus nova-caesariensis* Alex.

Tribe **Limnophilini**

Genus *Adelphomyia* Bergroth

Adelphomyia americana Alex.

Cortland County: Taylor, July 20 (C. P. A.).
Fulton County: Woodworth's Lake, August 22 (C. P. A.), T. L.; Johnstown, September 15–23 (C. P. A.); etc.
Hamilton County: Wells, July 29 (D. B. Y.).
Tompkins County: Ithaca, September 10 (C. P. A.).

Genus *Adelphomyia* Bergroth (*continued*)

A. cayuga Alex.

Tompkins County: Vanishing Brook, Ithaca, August 16 (C. P. A.), T. L.

A. minuta Alex.

Fulton County: Sacandaga Park, June 1–15 (C. P. A.); etc.

Herkimer County: Indian Castle, June 9 (C. P. A.).

Tompkins County: Ithaca, May 12–23 (C. P. A.), T. L.; McLean, June 5 (C. P. A.).

Genus *Limnophila* Macquart

Subgenus *Lasiomastix* Osten Sacken

Limnophila macrocera (Say)

Albany County: Karner, June 19 (D. B. Y.); Pine Hills, July 1 (D. B. Y.).

Cattaraugus County: Little Valley, July 18 to August 7 (M. C. VD.).

Chenango County: Lower Cincinnatus, July 21 (C. P. A.).

Cortland County: Taylor, July 20 (C. P. A.).

Erie County: Lancaster, May 31 (M. C. VD.); Gowanda, June 14 (M. C. VD.); etc.

Franklin County: Axton, June (A. D. M.).

Fulton County: Sacandaga Park, June 11 to August 24 (C. P. A.); etc.

Hamilton County: Wells, July 20 (D. B. Y.).

Herkimer County: Indian Castle, June 9 (C. P. A.).

Onondaga County: Manlius, August 18 (H. H. S.).

Suffolk County: Yaphank, May 29.

Tompkins County: Ithaca, May 23–26 (C. P. A.); McLean, June 5 (C. P. A.); etc.

Westchester County: Tarrytown, June 9 (S. W. F.).

L. subtenuicornis (Alex.)

Tompkins County: McLean, May 31 (C. P. A.); Ithaca, June 4–13 (C. P. A.), T. L.

L. tenuicornis O. S.

Fulton County: Mountain Lake, June 17–19 (C. P. A.); Gloversville, June 24 (C. P. A.).

Herkimer County: Indian Castle, June 9 (C. P. A.).

Tompkins County: Ithaca, May 20–29 (C. P. A.); McLean, June 5 (C. P. A.).

Subgenus *Idioptera* Macquart

Limnophila fasciolata O. S.

Albany County: Albany, June 17 (D. B. Y.).

Tompkins County: McLean, June 5 (C. P. A.).

Subgenus *Limnophila* Macquart

Limnophila adusta O. S.

Cayuga County: North Fair Haven, September 12 (C. P. A.).

Erie County: Lancaster, May 31 (M. C. VD.); Buffalo, June 10–12 (M. C. VD.); etc.

Essex County: Wilmington, August 24 (J. C. B.).

Fulton County: Mount Buell, June 5 to July 7 (C. P. A.); etc.

Genesee County: Batavia, August 6 (H. H. K.).

Onondaga County: Green Lake, June 8 (C. P. A.); Manlius, September 6 (H. H. S.).

Schenectady County: Schenectady, June 14 (A. O.).

Tompkins County: Ithaca, May 21 to June 5 (C. P. A.); etc.

L. albipes Leon.

Fulton County: Mountain Lake, altitude 1590 feet, July 7 (C. P. A.).

Westchester County: Tarrytown, June 16 (S. W. F.).

Genus *Limnophila* Macquart (*continued*)
Subgenus *Limnophila* Macquart (*continued*)

L. alleni Johns.
Albany County: Karner, June 19 (D. B. Y.).
Fulton County: Gloversville, June 9–22 (C. P. A.).
Tompkins County: Ithaca, June 20 (A. H. M.); etc.

L. areolata O. S.
Albany County: Helderbergs, June 12 (C. P. A.); Albany, June 26 (D. B. Y.).
Cattaraugus County: Rock City, June 6 (J. C. B.).
Erie County: Gowanda, June 14 (M. C. VD.); Hamburg, June 18 (M. C. VD.); etc.
Essex County: Uphill Creek and Opalescent River, foot of Mount Marcy, July 10 (C. R. C.).
Fulton County: Mountain Lake, June 3–29 (C. P. A.); etc.
Hamilton County: Mount Buell, June 13 (C. P. A.).
Herkimer County: Trenton Falls (O. S.), T. L.; Old Forge, June 20 (J. G. N.).
Onondaga County: Green Lake, June 8 (C. P. A.).
Tompkins County: Ithaca, May 20 to June 5 (C. P. A.); etc.

L. brevifurca O. S.
Erie County: Holland, May 21 (M. C. VD.); Colden, May 23 (M. C. VD.).
Fulton County: Sacandaga Park, June 1–17 (C. P. A.); Gloversville, June 3–15 (C. P. A.); etc.
Herkimer County: Indian Castle, June 9 (C. P. A.); Old Forge, August (J. G. N.).
Tompkins County: McLean, May 13 to June 5 (C. P. A.); Ithaca, May 14–21 (C. P. A.); etc.

L. contempta O. S.
Fulton County: Sacandaga Park, July 3 (C. P. A.).

L. edwardi Alex.
Fulton County: Gloversville, June 22 (C. P. A.), T. L.

L. emmelina Alex.
Fulton County: Mount Buell, altitude 1600 feet, June 18 (C. P. A.).

L. fratria O. S.
Erie County: East Aurora, May 18 (M. C. VD.). (Van Duzee, auct.)
(The type-locality for *L. fratria* was supposed by Osten Sacken to be New York State.)

L. imbecilla O. S.
Erie County: Gowanda, June 7–14 (M. C. VD.); Buffalo, June 12–15 (M. C. VD.).
Fulton County: Sacandaga Park, June 26 (C. P. A.).
Genesee County: Batavia, August 1 (H. H. K.).
Herkimer County: Trenton Falls (O. S.), T. L.
Westchester County: Tarrytown, June 9 (S. W. F.).

L. inornata O. S.
Fulton County: Sacandaga Park, June 1–11 (C. P. A.).
Herkimer County: Old Forge, August (J. G. N.).
Onondaga County: Green Lake, June 8 (C. P. A.).
Oswego County: Oswego, July 17.
Tompkins County: Ithaca, reared May 25 (C. P. A.).

L. laricicola Alex.
Fulton County: Canada Lake, June 20 (C. P. A.), T. L.

L. lenta O. S.
Cayuga County: North Fair Haven, September 12 (C. P. A.).
Chenango County: Lower Cincinnatus, July 21 (C. P. A.).
Cortland County: Taylor, July 20 (C. P. A.).

Genus *Limnophila* Macquart (*continued*)
Subgenus *Limnophila* Macquart (*continued*)
L. lenta O. S. (*continued*)
Erie County: Hamburg, May 26 (M. C. VD.); South Wales, July 9 (M. C. VD.); etc.
Fulton County: Johnstown, June 26 to September 2 (C. P. A.); etc.
Hamilton County: Wells, July 29 (D. B. Y.); Dug Mountain, August 8 (D. B. Y.).
Onondaga County: Green Lake, June 8 (C. P. A.).
Saratoga County: Corinth, June 23 (D. B. Y.).
Tompkins County: Ithaca, May 26 to August 12 (C. P. A.).
L. lutea Doane
Tompkins County: McLean, May 31 (F. K.).
L. luteipennis O. S.
Albany County: Karner, June 13 (D. B. Y.).
Chenango County: Lower Cincinnatus, July 21 (C. P. A.).
Cortland County: Taylor, July 20 (C. P. A.).
Erie County: Colden, May 23 (M. C. VD.); Hamburg, May 26 (M. C. VD.).
Fulton County: Sacandaga Park, June 1 to August 24 (C. P. A.); etc.
Greene County: New Baltimore, September 17 (D. B. Y.).
Herkimer County: Indian Castle, June 9 (C. P. A.).
Nassau County: Sea Cliff (N. B.).
Tompkins County: Ithaca, May 7 to June 5 (C. P. A.); etc.
L. nigripleura A. & L.
Chenango County: Lower Cincinnatus, July 21 (C. P. A.).
Cortland County: Taylor, July 20 (C. P. A.).
Fulton County: Mountain Lake, June 17 to August 13 (C. P. A.); etc.
Herkimer County: Indian Castle, June 13 (C. P. A.).
Nassau County: Sea Cliff (N. B.).
Tompkins County: Ithaca, May 31 (R. H. T.); etc.
L. niveitarsis O. S.
Fulton County: Mount Buell, altitude 1400 feet, June 18–29 (C. P. A.).
Herkimer County: Old Forge, July 20 (J. G. N.).
L. noveboracensis Alex.
Albany County: Albany, June 26 (D. B. Y.).
Cortland County: Taylor, July 20 (C. P. A.).
Fulton County: Sacandaga Park, June 21–28 (C. P. A.), T. L.; etc.
Rockland County: West Nyack, June 15 (W. S.).
Tompkins County: Ithaca, July 11–12 (C. P. A.).
L. quadrata O. S.
Albany County: Albany, June 7 (D. B. Y.).
Chenango County: Lower Cincinnatus, July 21 (C. P. A.).
Erie County: Hamburg, May 22 to June 6 (M. C. VD.); Buffalo, June 15 (M. C. VD.); etc.
Fulton County: Sacandaga Park, June 5 to July 7 (C. P. A.); etc.
Genesee County: Batavia, June 6 (H. H. K.).
Onondaga County: Green Lake, June 8 (C. P. A.).
Tompkins County: Ithaca, May 21–29 (C. P. A.), July 25 (H. Y.); McLean, June 5 (C. P. A.); Ringwood Hollow, July 14 (H. Y.).
Westchester County: Tarrytown, June 9 (S. W. F.).
L. recondita O. S.
Albany County: Albany, June 15 (D. B. Y.).
Erie County: Buffalo, June 10 (M. C. VD.).
Fulton County: Sacandaga Park, June 21–28 (C. P. A.); etc.
Herkimer County: Indian Castle, June 9 (C. P. A.).

Genus *Limnophila* Macquart (*continued*)
Subgenus *Limnophila* Macquart (*continued*)
L. recondita O. S. (*continued*)
Rockland County: West Nyack, June 15 (W. S.).
Tompkins County: Ithaca, May 26–29 (C. P. A.); McLean, June 5 (C. P. A.). (Osten Sacken's T. L. is New York State.)
L. similis Alex.
Fulton County: Johnstown, June 10–26 (C. P. A.), T. L.; Sacandaga Park, June 29 (C. P. A.).
Hamilton County: Wells, July 7 (D. B. Y.).
L. stanwoodae Alex.
Fulton County: Sacandaga Park, June 11 (C. P. A.), T. L.
L. subcostata (Alex.)
Fulton County: Sacandaga Park, June 1 (C. P. A.); Gloversville, June 3–9 (C. P. A.).
Herkimer County: Indian Castle, June 9 (C. P. A.).
Tompkins County: Ithaca, May 7–31 (C. P. A.), T. L.; etc.
L. sylvia Alex.
Fulton County: Mountain Lake, altitude 1590 feet, June 13 (C. P. A.), T. L.
L. tenuipes (Say)
Albany County: Albany, June 26 (D. B. Y.).
Cortland County: Cincinnatus, July 21 (C. P. A.).
Erie County: Hamburg, May 28 (M. C. VD.); Colden, June 7 (M. C. VD.); Elma, August 27 (M. C. VD.); etc.
Fulton County: Sacandaga Park, June 15 to August 24 (C. P. A.).
Onondaga County: Manlius, September 6 (H. H. S.).
Rockland County: West Nyack, June 15 (W. S.).
Tompkins County: Ithaca, May 20 to August 12 (C. P. A.); McLean, June 5 (C. P. A.).
L. toxoneura O. S.
Albany County: Helderbergs, July 3 (C. P. A.).
Cattaraugus County: Little Valley, June 30 (M. C. VD.).
Chenango County: Lower Cincinnatus, July 21 (C. P. A.).
Fulton County: Mount Buell, June 13–29 (C. P. A.); Gloversville, June 14–24 (C. P. A.); etc.
Hamilton County: Mount Buell, June 13 (C. P. A.).
Herkimer County: Trenton Falls (O. S.), T. L.; Indian Castle, June 9 (C. P. A.); Old Forge, August (J. G. N.).
Onondaga County: Green Lake, June 8 (C. P. A.).
Rensselaer County: Brookview, July 9 (M. M. A.).
L. ultima O. S.
Albany County: Albany, May 15, October 4–7 (D. B. Y.).
Cattaraugus County: Olean, September 5 (C. R. C.).
Erie County: Colden, August 7 (M. C. VD.).
Fulton County: Woodworth's Lake, August 12 (C. P. A.); Gloversville, September 15–17 (C. P. A.).
Hamilton County: Middle Lake, Hope Township, September 12 (C. P. A.).
Monroe County: Rochester, October 10 (M. C. VD.).
Tompkins County: May 8, October 12 (C. P. A.).
Subgenus *Ephelia* Schiner
Limnophila aprilina O. S.
Albany County: Karner, June 15 (D. B. Y.).
Chenango County: Lower Cincinnatus, July 21 (C. P. A.).
Cortland County: Taylor, July 20 (C. P. A.).

Genus *Limnophila* Macquart (*continued*)

Subgenus *Ephelia* Schiner (*continued*)

Limnophila aprilina O. S. (*continued*)

Erie County: Gowanda, June 27 (M. C. VD.); South Wales, July 9 (M. C. VD.).
Fulton County: Mountain Lake, June 15 to July 7 (C. P. A.).
Hamilton County: Wells, July 29 (D. B. Y.).
Tompkins County: Ithaca, May 12–29 (C. P. A.).

L. johnsoni Alex.

Fulton County: Mount Buell, June 15 (C. P. A.); Mountain Lake, altitude 1600 feet, June 17 (C. P. A.), T. L.
Tompkins County: Coy Glen, Ithaca, May 23 (C. P. A.).

Subgenus *Dicranophragma* Osten Sacken

Limnophila fuscovaria O. S.

Albany County: Karner, June 13 (D. B. Y.).
Chenango County: Lower Cincinnatus, July 21 (C. P. A.).
Cortland County: Taylor, July 20 (C. P. A.).
Erie County: Hamburg, June 6–20 (M. C. VD.); Gowanda, June 7 (M. C. VD.); etc.
Fulton County: Sacandaga Park, June 15 to August 24 (C. P. A.); etc.
Hamilton County: Wells, July 23 (D. B. Y.).
Herkimer County: Indian Castle, June 9 (C. P. A.).
Queens County: Flushing, June 22 (C. R. P.).
Tompkins County: Ithaca, May 17 to August 12 (C. P. A.); Norton's Landing, June 24 (H. H. S.).
Westchester County: Tarrytown, June 9 (S. W. F.).
Wyoming County: Portage, May 24 (H. H. K.).

Subgenus *Prionolabis* Osten Sacken

Limnophila munda O. S.

Cattaraugus County: Mix Creek Valley, June 11 (J. C. B.).
Essex County: Uphill Creek and Opalescent River, foot of Mount Marcy, July 10 (C. R. C.).
Fulton County: Mount Buell, June 13–29 (C. P. A.); Gloversville, June 16 (C. P. A.); etc.

L. rufibasis O. S.

Albany County: Albany, May 26 to June 5 (D. B. Y.).
Clinton County: Peru, June 23 (C. R. C.).
Erie County: Holland, May 21 (M. C. VD.); Lancaster, May 31 (M. C. VD.); etc.
Fulton County: Gloversville, May 20 to June 3 (C. P. A.); Mount Buell, June 13–17 (C. P. A.); etc.
Hamilton County: Mount Buell, June 13 (C. P. A.).
Herkimer County: Indian Castle, June 13 (C. P. A.).
Oneida County: Remsen, June 5 (W. A. C.).
Tompkins County: Ithaca, May 4–31 (C. P. A.); Norton's Landing, June 2 (H. H. S.); McLean, June 5 (C. P. A.).
Wyoming County: Portage, May 24 (H. H. K.).

L. simplex Alex.

Fulton County: Woodworth's Lake, June 17 (C. P. A.).

Subgenus *Dactylolabis* Osten Sacken

Limnophila cubitalis O. S.

Cattaraugus County: Rock City, June 6–10 (J. C. B. and H. H. K.).
Tompkins County: Ithaca, May 7–30 (C. P. A.); Taughannock Falls, May 19 (C. P. A.).

Genus *Limnophila* Macquart (*continued*)
Subgenus *Dactylolabis* Osten Sacken (*continued*)
L. montana O. S.
Albany County: Helderbergs, June 12 (C. P. A.).
Cattaraugus County: Little Valley, June 30 (M. C. VD.).
Erie County: Spring Brook, June 25 (M. C. VD.).
Fulton County: Mount Buell, June 13–18 (C. P. A.); etc.
Herkimer County: Little Falls, June 9 (C. P. A.).
New York: (O. S.), T. L.
Niagara County: Niagara Falls, June 9 (M. C. VD.).
Tompkins County: Ithaca, May 5–24 (C. P. A.).

Genus *Epiphragma* Osten Sacken
Epiphragma fascipennis (Say)
Albany County: Helderbergs, June 12 (C. P. A.); Albany, June 19–25 (D. B. Y.).
Cattaraugus County: Rock City, June 6–7 (J. C. B. and H. H. K.); Vandalia, June 9 (C. R. C.).
Erie County: Colden, May 23 to June 7 (M. C. VD.); Buffalo, June 10–23 (M. C. VD.); etc.
Fulton County: Sacandaga Park, June 1–21 (C. P. A.); etc.
Herkimer County: Indian Castle, June 9 (C. P. A.); Old Forge, June 20 (J. G. N.).
Nassau County: Sea Cliff (N. B.).
Oneida County: Cincinnati Creek, May 26 (W. A. C.).
Onondaga County: Green Lake, June 8 (C. P. A.).
Queens County: Flushing, June 22 (C. R. P.).
Tompkins County: Ithaca, May 14–30 (C. P. A.); McLean, June 5 (C. P. A.).
Westchester County: Tarrytown, June 9 (S. W. F.).
E. solatrix (O. S.)
Nassau County: Sea Cliff, June (N. B.).

Genus *Ula* Haliday
Ula elegans O. S.
Fulton County: Pinnacle Mountain, September 16 (C. P. A.); etc.
Herkimer County: Old Forge, August (J. G. N.).
Tompkins County: Ithaca, May 13 to June 20 (C. P. A.).
U. paupera O. S.
Erie County: Holland, May 21 (M. C. VD.); East Aurora, June 22 to August 24 (M. C. VD.).
Fulton County: Johnstown, May 13 (C. P. A.); etc.
Tompkins County: Ithaca, May 13 (C. P. A.).

Genus *Ulomorpha* Osten Sacken
Ulomorpha pilosella (O. S.).
Chenango County: Lower Cincinnatus, July 21 (C. P. A.).
Cortland County: Taylor, July 20 (C. P. A.).
Erie County: East Aurora, June 11 (M. C. VD.); South Wales, July 9 (M. C. VD.); Boston, July 10 (M. C. VD.).
Fulton County: Gloversville, June 3–9 (C. P. A.); Mountain Lake, June 13–17 (C. P. A.).
Herkimer County: Trenton Falls (O. S.), T. L.; Indian Castle, June 9 (C. P. A.).
Oneida County: Cyrus Brook, July 10 (W. A. C.).
Schoharie County: Sharon Springs (O. S.), T. L.
Tompkins County: McLean, June 5 (C. P. A.); Ithaca, June 20 (L. W. C.).

Regional species: *Limnophila irrorata* Johns., *L. marchandi* Alex., *L. mundoides* Alex., *L. novae-angliae* Alex., *L. osborni* Alex., *L. poetica* O. S., *L. unica* O. S.

Tribe Hexatomini

Genus *Penthoptera* Schiner

Penthoptera albitarsis O. S.

Chenango County: Lower Cincinnatus, July 21 (C. P. A.).
Erie County: South Wales, July 9 (M. C. VD.); Hamburg, July 10 (M. C. VD.); Boston, July 10 (M. C. VD.).
Fulton County: Sacandaga Park, June 27 (C. P. A.); Woodworth's Lake, July 19 (C. P. A.).
Tompkins County: Ithaca, July 11 to August 12 (C. P. A.), September 17 (J. G. N.).

Genus *Eriocera* Macquart

Eriocera brachycera O. S.

Chenango County: Lower Cincinnatus, July 21 (C. P. A.).
Cortland County: Near Lower Cincinnatus, July 21 (C. P. A.).
Erie County: South Wales, July 9 (M. C. VD.); Colden, July 25 (M. C. VD.).
Fulton County: Pinnacle Mountain, altitude 2000 feet, August 4 (C. P. A.).
Herkimer County: Old Forge, July 12–16 (J. G. N.).

E. cinerea Alex.

Fulton County: Woodworth's Lake, June 15 (C. P. A.).
Tompkins County: Ithaca, reared from larvae, May 16 (C. P. A.); Bear Creek, Freeville, May 16 (C. P. A.); Norton's Landing, May 25 (H. H. S.).

E. fuliginosa O. S.

Erie County: North Evans, May 25 to July 4 (M. C. VD.); Colden, May 31 (M. C. VD.); etc.
(Determined by Van Duzee; species not seen by writer.)

E. fultonensis Alex.

Fulton County: Sport Island, Sacandaga River, altitude 750 feet, June 15–27 (C. P. A.).
Tompkins County: Ithaca, reared May 30 to June 6 (J. T. L.), June 13 (C. P. A.), June 23 (H. Y.).

E. longicornis (Walk.)

Albany County: Albany, May 6 (D. B. Y.).
Erie County: North Evans, May 14 (M. C. VD.).
Fulton County: Fish-House, May 28 (C. P. A.); etc.
Herkimer County: Trenton Falls (O. S.); Dolgeville, May 16 (C. P. A.).
Tompkins County: Ithaca, May 1–30 (C. P. A. and J. G. N.); etc.

E. spinosa (O. S.)

Cortland County: Lower Cincinnatus, July 21 (C. P. A.).
Fulton County: Sacandaga Park, June 5 (C. P. A.).
Herkimer County: Trenton Falls (O. S.), T. L.
Oneida County: Tannery Brook, September 9 (larvae) (W. A. C.).
Tompkins County: Ithaca, May 17 to August 5; etc.

E. tristis Alex.

Tompkins County: Ithaca, August 1 (C. P. A. and C. I.), T. L.

Genus *Hexatoma* Latreille

Hexatoma megacera (O. S.)

Fulton County: Johnstown, May 24 (C. P. A.); Sport Island, Sacandaga River, June 15 (C. P. A.); etc.
Tompkins County: Ithaca, May 15 (C. P. A.); North Lansing, June 1 (S. C. B.); etc.

Regional species: *Eriocera wilsonii* O. S.

Tribe **Pediciini**

Genus *Pedicia* Latreille
Pedicia albivitta Walk.
Albany County: Indian Ladder, Helderbergs, July 3 (C. P. A.).
Broome County: Binghamton.
Chenango County: Lower Cincinnatus, July 21 (C. P. A.).
Cortland County: Taylor, July 20 (C. P. A.).
Erie County: South Wales, July 9 (M. C. VD.); East Aurora, August 15 to September 11 (M. C. VD.); etc.
Fulton County: Gloversville, June 11 (A. O.); Mountain Lake, August 22 (C. P. A.); etc.
Hamilton County: Middle Lake, September 12 (C. P. A.).
Herkimer County: Trenton Falls (O. S.).
Onondaga County: Manlius, August 27 (H. H. S.); Baldwinsville, September
Tompkins County: Ithaca, August 1–12 (C. P. A.); etc.
Ulster County: Big Indian Valley, May 24 to August 23 (R. F. P.)
Westchester County: Mosholu.
P. *contermina* Walk.
Tompkins County: McLean, May 13 (C. P. A.); Ithaca, June 1 (C. R. P.); June 6 (S. A. G.).

Genus *Tricyphona* Zetterstedt
Tricyphona auripennis (O. S.)
Herkimer County: Indian Castle, June 10–13 (C. P. A.).
T. autumnalis Alex.
Cayuga County: North Fair Haven, September 12 (C. P. A.).
Erie County: Grand Island, September 6 (M. C. VD.).
Essex County: Mount Marcy, July 30 (D. B. Y.).
Fulton County: Pinnacle Mountain, August 5 (C. P. A.); Woodworth's Lake, September (C. P. A.), T. L.
Hamilton County: Elm Lake, August 2 (D. B. Y.); Dug Mountain, August 8 (D. B. Y.).
(Needham's record for *T. calcar*, Old Forge, August, probably belongs here.)
T. *calcar* (O. S.)
Cattaraugus County: Four-Mile, altitude 2300 feet, June 6 (J. C. B.).
Erie County: Colden, May 23 (M. C. VD.).
Essex County: Uphill Creek and Opalescent River, foot of Mount Marcy, July 10 (C. R. C.).
Fulton County: Sacandaga Park, June 1; Gloversville, June 3 (C. P. A.); etc.
Herkimer County: Newport, June 6 (D. B. Y.).
Tompkins County: McLean, May 22 to June 5 (C. P. A.); etc.
T. *inconstans* (O. S.)
Chenango County: Lower Cincinnatus, July 21 (C. P. A.).
Columbia County: Claverack, September 28 (J. S.).
Cortland County: Taylor, July 20 (C. P. A.).
Erie County: Hamburg, May 31 to June 20 (M. C. VD.); Boston, September 3 (M. C. VD.); etc.
Essex County: Uphill Creek and Opalescent River, foot of Mount Marcy, July 10 (C. R. C.).
Fulton County: Gloversville, June 10–27 (C. P. A.); Sacandaga Park, June 16 to August 24 (C. P. A.); etc.
Genesee County: Batavia, June 6 (H. H. K.).
Hamilton County: Mount Buell, June 13 (C. P. A.,

Genus *Tricyphona* Zetterstedt (*continued*)

T. inconstans (O. S.) (*continued*)

Herkimer County: Indian Castle, June 9 (C. P. A.); Old Forge, August (J. G. N.); Newport, August 31 (D. B. Y.).
Onondaga County: Manlius, September 10 (H. H. S.).
Monroe County: Rochester, October 10 (M. C. VD.).
Nassau County: Sea Cliff (N. B.).
Queens County: Rockaway Beach, June 26.
Schenectady County: Schenectady, June 14 (A. O.).
Tompkins County: Ithaca, May 12 to September 28 (C. P. A.); etc.
Westchester County: Tarrytown, June 9 (S. W. F.).
Wyoming County: Portage, May 24 (H. H. K.); Portageville, June 13 (C. R. C.).

T. paludicola Alex.

Tompkins County: McLean, May 13-20 (C. P. A. and P. W. C.), T. L.; Bear Creek, Freeville, May 16 (C. P. A.).

T. vernalis (O S.)

Fulton County: Mountain Lake, June 13-15 (C. P. A.); Mount Buell, June 15 (C. P. A.).
Herkimer County: Indian Castle, June 13 (C. P. A.).
Nassau County: Sea Cliff, April (N. B.).
Tompkins County: Forest Home, May 7 (S. W. F.); Taughannock, May 8 (R. H. T.).

Genus *Dicranota* Zetterstedt

Dicranota noveboracensis Alex.

Fulton County: Dolgeville, May 16 (C. P. A.), T. L.
Tompkins County: Ithaca, April 24 (S. W. F.); May 8 (C. P. A.); etc.

D. rivularis O. S.

Tompkins County: Ithaca, April 21 (C. R. P.).

Genus *Rhaphidolabis* Osten Sacken

Subgenus *Rhaphidolabina* Alexander

Rhaphidolabis flaveola O. S.

Chenango County: Lower Cincinnatus, July 21 (C. P. A.).
Erie County: Hamburg, May 28 (M. C. VD.).
Fulton County: Gloversville, June 3–15 (C. P. A.); Mount Buell, June 13–17 (C. P. A.); Woodworth's Lake, August 22 (C. P. A.).
Hamilton County: Wells, July 9 (D. B. Y.).
Herkimer County: Indian Castle, June 9 (C. P. A.); Old Forge, August (J. G. N.).
Tompkins County: Ithaca, May 30–31 (C. P. A.); etc.

Subgenus *Rhaphidolabis* Osten Sacken

Rhaphidolabis cayuga Alex.

Fulton County: Johnstown, August 19 (C. P. A.); Mountain Lake, September 2 (C. P. A.).
Tompkins County: Ithaca, April 22 (J. G. N.); McLean, May 13 (C. P. A.), T. L.

R. rubescens Alex.

Fulton County: Gloversville, altitude 900 feet, June 22 (C. P. A.), T. L.

R. tenuipes O. S.

Albany County: Indian Ladder, Helderbergs, July 3 (C. P. A.).
Cattaraugus County: Little Valley, June 30 (M. C. VD.).
Erie County: North Evans, May 14 (M. C. VD.); Holland, May 21 (M. C. VD.).

Genus *Rhaphidolabis* Osten Sacken (*continued*)

Subgenus *Rhaphidolabis* Osten Sacken (*continued*)

R. tenuipes O. S. (*continued*)

Fulton County: Gloversville, May 13 to August 5 (C. P. A.); etc.
Herkimer County: Indian Castle, June 13 (C. P. A.); Old Forge, August 6 (J. G. N.).
Oneida County: Field's Brook, August 30 (W. A. C.).
Saratoga County: Saratoga Springs (O. S.), T. L.
Tompkins County: Ithaca, May 1 to August 12 (J. G. N.).

Subgenus *Plectromyia* Osten Sacken

Rhaphidolabis modesta (O. S.)

Erie County: Holland, May 21 (M. C. VD.). (Van Duzee, auct.)
Fulton County: Mountain Lake, altitude 1600 feet, June 13 (C. P. A.).

Regional species: *Dicranota eucera* O. S., *D. pallida* Alex., *Tricyphona hyperborea* (O. S.) *T. katahdin* Alex.

Subfamily **Cylindrotominae**

Genus *Cylindrotoma* Macquart

Cylindrotoma tarsalis Johns.

Fulton County: Gloversville, June 9 (C. P. A.); Woodworth's Lake, altitude 1650 feet, June 17 to August 19 (C. P. A.), T. L.
Herkimer County: Indian Castle, June 13 (C. P. A.).

Genus *Liogma* Osten Sacken

Liogma nodicornis (O. S.)

Erie County: Hamburg, May 28 to June 20 (M. C. VD.); Colden, June 7 (M. C. VD.); etc.
Fulton County: Sacandaga Park, June 15–26 (C. P. A.); etc.
Herkimer County: Indian Castle, June 9 (C. P. A.).
Onondaga County: Green Lake, June 8 (C. P. A.).
Tompkins County: North Lansing, June 1 (C. R. C.); Ithaca, June 10–14 (C. P. A.).
Westchester County: Tarrytown, June 9 (S. W. F.).

Genus *Phalacrocera* Schiner

Phalacrocera neoxena Alex.

Cayuga County: North Fair Haven, May 17, dead in lake drift (J. G. N. and E. M.), T. L.

P. tipulina O. S.

Essex County: Lake Tear of the Clouds, Mount Marcy, July 10 (C. R. C.).
Fulton County: Near Sacandaga Park, June 18 (C. P. A.); Canada Lake, June 23 to July 10 (C. P. A.); etc.
Herkimer County: Old Forge, July, August 3 (J. G. N.).
Tompkins County: Ringwood Hollow, July 3 (H. Y.).

Regional species: *Cylindrotoma americana* O. S., *Triogma exculpta* O. S.

Subfamily **Tipulinae**

Tribe **Dolichopezini**

Genus *Dolichopeza* Curtis

Dolichopeza americana Needm.

Cattaraugus County: Little Valley, June 30 (M. C. VD.).
Fulton County: Sacandaga Park, June 1–15 (C. P. A.); Mountain Lake, June 13–17 (C. P. A.).

Genus *Dolichopeza* Curtis (*continued*)
Dolichopeza americana Needm. (*continued*)
Herkimer County: Old Forge, August (J. G. N.), T. L.
Queens County: Flushing, June 22 (C. R. P.).

Genus *Oropeza* Needham
Oropeza albipes Johns.
Cattaraugus County: Four-Mile, July 4 (H. H. K.).
Cortland County: Taylor, July 20 (C. P. A.).
Erie County: Colden, July 3 (M. C. VD.); South Wales, July 9 (M. C. VD.); Boston, July 10 (M. C. VD.); etc.
Fulton County: Sacandaga Park, June 28 (C. P. A.).
Herkimer County: Old Forge, June 20 (J. G. N.).
Suffolk County: Bellport, August 9.
Westchester County: Tarrytown, June 9 (S. W. F.).
O. obscura Johns.
Albany County: Helderbergs, July 3 (C. P. A.).
Cattaraugus County: Little Valley, June 30 (M. C. VD.); Four-Mile, July 4 (H. H. K.).
Chenango County: Lower Cincinnatus, July 21 (C. P. A.).
Cortland County: Taylor, July 20 (C. P. A.).
Erie County: East Aurora, June 16 (M. C. VD.); South Wales, June 23 to July 9 (M. C. VD.).
Fulton County: Woodworth's Lake, June 15 to August 20 (C. P. A.); etc.
Hamilton County: Wells, July 30 (D. B. Y.).
Tompkins County: Ringwood Hollow, July 6 (H. Y.).
Warren County: County-Line Flow, Griffin, July 26 (C. P. A.).
O. sayi Johns.
Erie County: South Wales, July 9 (M. C. VD.); Boston, July 10 (M. C. VD.).
Herkimer County: Old Forge, August (J. G. N.).
Niagara County: Niagara Falls, June 23.
Tompkins County: Ithaca, August (J. G. N.).
O. similis Johns.
Erie County: Gowanda, June 7–14 (M. C. VD.); Elma, August 20 (M. C. VD.).
O. subalbipes Johns.
Erie County: South Wales, July 9 (M. C. VD.).
Westchester County: Tarrytown, June 9 (S. W. F.)
O. venosa Johns.
Cattaraugus County: Little Valley, June 30 (M. C. VD.).
Cortland County: Lower Cincinnatus, July 21 (C. P. A.).
Erie County: South Wales, June 23 (M. C. VD.).
Fulton County: Mountain Lake, June 15–17 (C. P. A.); Northampton, June 25 (D. B. Y.); etc.
Herkimer County: Indian Castle, June 9 (C. P. A.).
Tompkins County: McLean, June 5 (C. P. A.).

Regional species: *Brachypremna dispellens* (Walk.), *Oropeza dorsalis* Johns.

Tribe **Ctenophorini**

Genus *Tanyptera* Latreille
Tanyptera frontalis (O. S.)
Cattaraugus County: Rock City, June 16 (J. C. B. and W. T. M. F.).
Fulton County: Mountain Lake, June 13 (C. P. A.).
Tompkins County: Ithaca, May 30–31 (C. I.).

Genus *Tanyptera* Latreille (*continued*)
T. fumipennis (O. S.)
Erie County: Colden, May 30 (M. C. VD.).
Tompkins County: Ithaca, May 30–31 (C. I.).
T. topazina (O. S.)
Erie County: Lancaster, May 31 (M. C. VD.).
Tompkins County: Ithaca, May 31.

Genus *Ctenophora* Meigen
Ctenophora apicata O. S.
Fulton County: Mount Buell, altitude 1400 feet, June 29 (C. P. A.).
Suffolk County: Long Island, July.

Tribe **Tipulini**

Genus *Longurio* Loew
Longurio testaceus Loew
Chenango County: Near Lower Cincinnatus, July 21 (C. P. A.).
Cortland County: Lower Cincinnatus, July 21 (C. P. A.).
Fulton County: Gloversville, altitude 1000 feet, June 27 (C. P. A.).
Nassau County: Sea Cliff (N. B.).

Genus *Stygeropis* Loew
Stygeropis fuscipennis Loew
Albany County: Albany, August 6 (D. B. Y.).
Erie County: East Aurora, June 11 (M. C. VD.).
Fulton County: Sacandaga Park, June 29 (C. P. A.); Mountain Lake, August 13 (C. P. A.).
Tompkins County: Ithaca, July 10 (C. P. A.); Ringwood Hollow, larvae in November and May (C. H. K.).

Genus *Nephrotoma* Meigen
Nephrotoma breviorcornis (Doane)
Fulton County: Sacandaga Park, June 29 (C. P. A.).
N. calinota (Dietz)
Fulton County: Sacandaga Park, June 19 (C. P. A.).
N. eucera (Loew)
Fulton County: Sacandaga Park, June 11–16 (C. P. A.).
Onondaga County: Manlius, June 12 (H. H. S.).
Suffolk County: Long Island.
Tompkins County: Ithaca, June 29 to July 21.
N. ferruginea (Fabr.)
Albany County: Albany, June 7 (D. B. Y.); Helderbergs, July 3 (C. P. A.).
Cortland County: Gee Brook, July 20 (A. O.); Cincinnatus, July 21 (C. P. A.).
Erie County: Hamburg, May 28 (M. C. VD.); Buffalo, June 26 (J. G. N.); June 27 to November 11 (M. C. VD.); etc.
Fulton County: Sacandaga Park, June 1 to August 24 (C. P. A.); etc.
Genesee County: Batavia, September 3 (H. H. K.).
Herkimer County: Indian Castle, June 13 (C. P. A.).
Jefferson County: Alexandria Bay, September 3.
Monroe County: Honeoye Falls, July 4 to September 1 (C. R. C.).
Onondaga County: Baldwinsville, June 14; Manlius, August 18 (H. H. S.).
Ontario County: Clifton Springs, August 23.
Suffolk County: Astoria; Maspeth, June 1; Bellport, June 2; North Beach, September 18.
Sullivan County: White Lake, August 21 (J. L. Z.).
Tompkins County: Ithaca, May 7 to September 20 (C. P. A.); etc.

Genus *Nephrotoma* Meigen (*continued*)

N. gracilicornis (Loew)

Onondaga County: Manlius, August 8 (H. H. S.).

N. incurva (Loew)

Albany County: Albany, July 1 (D. B. Y.).
Cortland County: Taylor, July 20 (C. P. A.).
Erie County: East Aurora, June 12 to August 25 (M. C. VD.); South Wales, July 9–13 (M. C. VD.).
Essex County: Keene Valley, July 26 (J. A. L.).
Fulton County: Sacandaga Park, June 1–11 (C. P. A.); etc.
Genesee County: Batavia, July 22 (H. H. K.).
Greene County: New Baltimore, May 29 (D. B. Y.).
Hamilton County: Lake Placid, August 7 (J. A. L.).
Niagara County: Niagara Falls, June 9 (M. C. VD.).
Onondaga County: Manlius, August 24 (H. H. S.).
Tompkins County: Ithaca, June 18 to August 4 (C. P. A.); etc.

N. lugens (Loew)

Albany County: Karner, June 26 (D. B. Y.).
Cattaraugus County: Rock City, June 16 (H. H. K.).
Essex County: Elizabethtown, June 8 (D. B. Y.); Keene Valley, June 17 (J. A. L.).
Fulton County: Sacandaga Park, June 5-16 (C. P. A.); etc.
Genesee County: Batavia, July 19 (H. H. K.).
Herkimer County: Newport, May 29 (D. B. Y.); Indian Castle, June 13 (C.P. A.).
Steuben County: Lake Keuka, June 15 (C. R. C.).
Tompkins County: Ithaca, May 25 to June 29 (C. P. A.); Norton's Landing, June 2 (H. H. S.).

N. macrocera (Say)

Fulton County: Sacandaga Park, June 11–29 (C. P. A.); etc.
Westchester County: Tarrytown, June 16 (S. W. F.).

N. pedunculata (Loew)

Cattaraugus County: Four-Mile, July 4 (H. H. K.).
Cortland County: Taylor, July 20 (C. P. A.).
Essex County: Keene Valley, July 30 (J. A. L.).
Fulton County: Sacandaga Park, June 15 (C. P. A.).
Genesee County: Batavia, June 27 (H. H. K.).
Suffolk County: Long Island, July.

N. polymera (Loew)

Fulton County: Sacandaga Park, June 11–29 (C. P. A.).
Niagara County: Niagara Falls, June 9 (M. C. VD.).
Rensselaer County: Brookview, July 16 (M. M. A.)
Tompkins County: Ithaca, June 29.

N. sodalis (Loew)

Onondaga County: Baldwinsville, June 13.

N. tenuis (Loew)

Cattaraugus County: Rock City, June 16 to July 4 (H. H. K.).
Cortland County: Cincinnatus, July 21 (C. P. A.).
Dutchess County: Poughkeepsie, June 4 (D. B. Y.).
Erie County: Colden, July 10 (M. C. VD.); East Aurora, July 23 to August 21 (M. C. VD.); etc.
Fulton County: Sacandaga Park, June 11–27 (C. P. A.); etc.
Genesee County: Batavia, June 22 (H. H. K.).
Sullivan County: August (Dietz collection).
Tompkins County: Ithaca, July 4 to August 2.
Westchester County: Tarrytown, June 16 (S. W. F.).

Genus *Nephrotoma* Meigen (*continued*):

N. virescens (Loew)

Fulton County: Mountain Lake, altitude 1500 feet, August 13 (C. P. A.).
Tompkins County: Cascadilla Creek, near Ithaca, July 11 (H. Y.).

N. xanthostigma (Loew)

Erie County: Colden, August 7 (M. C. VD.); Lancaster, September 13 (M. C. VD.); etc.
Suffolk County: Yaphank, June 28 (A. M. N.); Cold Spring Harbor, July 15 (A. L. M.); Bellport, August 1.
Sullivan County: August, 1912 (Dietz collection).

Genus *Tipula* Linnaeus

Subgenus *Cinctotipula* Alexander

Tipula algonquin Alex.

Essex County: Keene Valley, July 29 (J. A. L.); Elizabethtown, August 25 (D. B. Y.).

T. unimaculata (Loew)

Essex County: New Russia, August (J. C. B.)
Fulton County: Sacandaga Park, August 24 (C. P. A.).
Hamilton County: Hope Township, September 12–13 (C. P. A.).
Onondaga County: Manlius, September 6 (H. H. S.).
Tompkins County: Norton's Landing, September 6 (H. H. S.).
Wayne County: Sodus, August 15.

Subgenus *Odontotipula* Alexander

Tipula unifasciata (Loew)

Onondaga County: Manlius, August 29 (H. H. S.).
Tompkins County: Norton's Landing, August 12 (H. H. S.).

Subgenus *Trichotipula* Alexander

Tipula oropezoides Johns.

Erie County: Hamburg, May 28 (M. C. VD.).
Fulton County: Sacandaga Park, June 1 (C. P. A.); Gloversville, June 6–28 (C. P. A.).
Herkimer County: Indian Castle, June 13 (C. P. A.).
Tompkins County: McLean, May 22 to June 5 (H. E. S.). Ithaca, May 29 to June 10 (C. P. A.).

Subgenus *Tipula* Linnaeus

Tipula abdominalis (Say)

Albany County: Coeymans, August 5.
Delaware County: Arkville, August (F. N. H.). (In Kansas University collection.)
Erie County: Gowanda, June 7–14, August 30 (M. C. VD.).
Essex County: Keene Valley, July 1 (J. A. L.); Lake Placid, August 19; New Russia, September 12–30 (J. C. B.).
Franklin County: Saranac Inn (J. G. N.).
Fulton County: Gloversville, July 29 to August 20 (Bromme).
Herkimer County: Old Forge, August 4 (J. G. N.).
Livingston County: Hemlock Lake, August 29 (C. R. C.).
Monroe County: Rochester Junction, June 9 (M. D. L.).
Oneida County: Brown Brook, July 14 (larvae) (W. A. C.).
Schoharie County: Sharon Springs (O. S.).
Suffolk County: Long Island, July.
Sullivan County: August (Dietz collection).
Tompkins County: Ithaca, August 30 to September 10.
Ulster County: Catskills, July (O. S.); Ellenville, August 10 (A. M. N.).
Wayne County: Newark, May 14.
Wyoming County: Portage, May 24 (H. H. K.).

Genus *Tipula* Linnaeus (*continued*)

Subgenus *Tipula* Linnaeus (*continued*)

T. afflicta Dietz

Erie County: South Wales, July 9 (M. C. VD.).

T. angustipennis Loew

Albany County: Karner, May 22 to June 13 (D. B. Y.); Albany, June 25 (D. B. Y.).
Erie County: Holland, May 21 (M. C. VD.).
Fulton County: Sacandaga Park, June 1–11 (C. P. A.); etc.
Herkimer County: Ilion, May 17 (D. B. Y.); Indian Castle, June 13 (C. P. A.).
Tompkins County: Ithaca, April 26 to June 20 (C. P. A.); etc.

T. apicalis Loew

Albany County: Albany, June 26 (D. B. Y.).
Essex County: Keene Valley, July 13 (J. A. L.).
Fulton County: Sacandaga Park, June 5–16 (C. P. A.).
Tompkins County: Ithaca, May 24–29; McLean, May 31 to June 5 (C. P. A.).
Westchester County: Dobbs Ferry (O. S.), T. L.

T. bella Loew

Albany County: Albany, June 7 (D. B. Y.).
Broome County: Binghamton (Dietz collection).
Cayuga County: North Fair Haven, September 12 (C. P. A.).
Erie County: North Evans, May 24 (M. C. VD.); East Aurora, August 21 (M. C. VD.); etc.
Fulton County: Sacandaga Park, June 1 to September 28 (C. P. A.); etc.
Genesee County: Batavia, September 1 (H. H. K.).
Greene County: New Baltimore, August 16 (D. B. Y.).
Monroe County: Honeoye Falls, September 1 (C. R. C.).
Nassau County: Sea Cliff, May (N. B.).
Oneida County: Remsen, July 5 (W. A. C.).
Onondaga County: Green Lake, June 8 (C. P. A.).
Queens County: May 16 to July.
Suffolk County: Bellport.
Tioga County: Willseyville, May 25 (W. A. H.).
Tompkins County: Ithaca, May 1 to September 10 (C. P. A.); etc.

T. bicornis Forbes

Erie County: East Aurora, June 11–16 (M. C. VD.); Lancaster, June 19 (M. C. VD.); etc.
Fulton County: Sacandaga Park, June 29 (C. P. A.).
Orange County: West Point (O. S.).
St. Lawrence County: Potsdam, June.
Tompkins County: McLean, May 31 (C. P. A.); Ithaca, June 5–12; July 3 (H. Y.); etc.

T. caloptera Loew

Erie County: North Evans, May 14 to June 28 (M. C. VD.); Colden, May 23 (M. C. VD.); etc.
Fulton County: Gloversville, May 18 to June 30 (C. P. A.); Sacandaga Park, June 1 (C. P. A.); etc.
Herkimer County: Indian Castle, June 13 (C. P. A.).
Niagara County: Niagara Falls, June 23 (M. C. VD.).
Oneida County: Mill Creek, July 7 (W. A. C.).
Rensselaer County: Brookview, July 16 (M. M. A).
Suffolk County: Yaphank, June 28 to September 2 (A. M. N.); Bellport, September.
Tompkins County: Ithaca, May 5–30 (C. P. A.); McLean, June 5 (C. P. A.); etc.
Wyoming County: Wyoming, June 25 (H. H. K.).

Genus *Tipula* Linnaeus (*continued*)

Subgenus *Tipula* Linnaeus (*continued*)

T. cayuga Alex.

Fulton County: Gloversville, June 9 (C. P. A.); T. L.
Herkimer County: Indian Castle, June 13 (C. P. A.).
Tompkins County: Ithaca, May 13–30 (C. P. A.).

T. collaris Say

Albany County: Albany, May 8 (D. B. Y.).
Cattaraugus County: Little Valley, June 30 (M. C. VD.).
Erie County: Colden, May 23 to July 1 (M. C. VD.); Gowanda, June 8 (M. C. VD.); etc.
Fulton County: Gloversville, June 9–24 (C. P. A.).
Herkimer County: Indian Castle, June 13 (C. P. A.).
Nassau County: Sea Cliff, May 20 (N. B.).
Tompkins County: Ithaca, May 3 to June 20 (C. P. A. and L. W. C.); etc.

T. cunctans Say

Cayuga County: North Fair Haven, September 12 (C. P. A.).
Erie County: Hamburg, September 11 to October 25 (M. C. VD.); Buffalo, September 25 to October 2 (M. C. VD.); etc.
Genesee County: Batavia, September 12–28 (H. H. K.).
Jefferson County: Alexandria Bay, September 3.
Kings County: Flatbush, September 13.
Niagara County: Niagara Falls, September 17 (M. C. VD.); Grand Island, October 4 (M. C. VD.).
Ontario County: Clifton Springs, September 12.
Tioga County: Owego, October 24 (H. H. K.).
Tompkins County: McLean, September 28 (C. R. C.); Ithaca, October 4.

T. dejecta Walk.

Albany County: Karner, April 25 (D. B. Y.); Albany, May 3 (D. B. Y.).
Erie County: Hamburg, May 14–22 (M. C. VD.); Colden, May 23–29 (M. C. VD.).
Fulton County: Gloversville, May 14 (C. P. A.).
Nassau County: Sea Cliff, May 1 (N. B.).
Tompkins County: Ithaca, April 26 to May 31 (C. P. A.).

T. eluta Loew

Dutchess County: Rhinebeck, July 27 (C. R. C.).
Erie County: Lancaster, May 31 (M. C. VD.); Elma, August 27 (M. C. VD.); etc.
Fulton County: Sacandaga Park, June 11–29 (C. P. A.).
Herkimer County: Indian Castle, June 9 (C. P. A.).
Tompkins County: Ithaca, May 24 (E. T. W.); etc.
Ulster County: Ellenville, July 20 (A. M. N.).

T. fragilis Loew

Erie County: Lancaster, September 24 (M. C. VD.); Buffalo, October 3 (M. C. VD.); etc.
Essex County: Lake Placid, altitude 2000 feet (Johnson collection).
Fulton County: Gloversville, September 7–20 (C. P. A.); etc.
Greene County: New Baltimore, September 17 (D. B. Y.).
Hamilton County: Big Notch Mountain, Hope Township, September 12 (C. P. A.).
Tompkins County: Ithaca, September 29 to October 9 (C. P. A.); Taughannock Falls, October 25 (C. R. C.).

T. fuliginosa (Say)

Albany County: Helderbergs, July 3 (C. P. A.).
Cattaraugus County: Rock City, June 16 (H. H. K.).

Genus *Tipula* Linnaeus (*continued*)

Subgenus *Tipula* Linnaeus (*continued*)

T. fuliginosa (Say) (*continued*)

Erie County: Lancaster, June 4 (M. C. VD.); East Aurora, June 11 (M. C. VD.); Colden, July 3 (M. C. VD.); etc.
Fulton County: Sacandaga Park, June 13–27 (C. P. A.).
Hamilton County: Mount Buell, June 13 (C. P. A.).
Herkimer County: Indian Castle, June 13 (C. P. A.).
Livingston County: Conesus Lake, June 22 (H. H. K.).
Tompkins County: McLean, June 5 (C. P. A.); Ithaca, June 20 to July 4 (C. P. A.).
Wyoming County: Portage, June 13–22 (H. H. K.).

T. fultonensis Alex.

Fulton County: Mount Buell, Sacandaga Park, altitude 1500 feet, June 15 (C. P. A.), T. L.

T. georgiana Alex.

Westchester County: New Rochelle (O. S.), T. L.

T. grata Loew

Erie County: Buffalo, August 5 (M. C. VD.).
Herkimer County: Old Forge, July 6 (J. G. N.).
Western New York: (O. S.), T. L.

T. hebes Loew

Cortland County: Taylor, July 20 (C. P. A.); Cincinnatus, July 21 (C. P. A.).
Erie County: Colden, August 3 (M. C. VD.); Hamburg, August 10 (M. C. VD.); East Aurora, August 21 (M. C. VD.).
Fulton County: Sacandaga Park, June 29 (C. P. A.); Johnstown, July 31 (C. P. A.).
Genesee County: Batavia, August 10 (H. H. K.).
Herkimer County: Old Forge, July 20 (J. G. N.).
Suffolk County: Cold Spring Harbor, July 15 (A. L. M.).
Tompkins County: Ithaca, August 2–26 (C. P. A.).
Warren County: County-Line Flow, Griffin, July 26 (C. P. A.); Lake George, August 17 (J. L. Z.).

T. helderbergensis Alex.

Albany County: Indian Ladder, Helderbergs, July 3 (C. P. A.), T. L.
Hamilton County: Wells, July 31 (D. B. Y.).

T. hermannia Alex.

Albany County: Albany, July 1 (D. B. Y.).
Cortland County: Taylor, July 20 (C. P. A.); Cincinnatus, July 21 (C. P. A.).
Essex County: Keene Valley, July 14 (J. A. L.); New Russia, August (J. C. B.).
Fulton County: Sacandaga Park, June 11 to August 24 (C. P. A.); etc.
Greene County: New Baltimore, August 16 (D. B. Y.).
Hamilton County: Wells, July 30 to August 31 (D. B. Y.); Speculator, August 27 (D. B. Y.).
Herkimer County: Indian Castle, June 13 (C. P. A.); Old Forge, August (J. G. N.).
Livingston County: Hemlock Lake, August 29 (C. R. C.).
Niagara County: Niagara Falls, June 28 (M. C. VD.).
Rockland County: Palisades (O. S.).
Schoharie County: Sharon Springs (O. S.), T. L.
Tompkins County: Ithaca, June 17 (J. G. N.); etc.
Ulster County: Catskills, July (O. S.).
Westchester County: Tarrytown, June 9 (S. W. F.).

T. hirsuta Doane

Fulton County: Mayfield Mountain, June 19 (C. P. A.).

Genus *Tipula* Linnaeus (*continued*)
Subgenus *Tipula* Linnaeus (*continued*)
T. ignobilis Loew
Albany County: Helderbergs, July 3 (C. P. A.).
Tompkins County: Ithaca, reared from larvae, May 21–26 (C. P. A.).
Ulster County: Catskills, July (O. S.).
T. iroquois Alex.
Fulton County: Mountain Lake, June 13 (C. P. A.); Gloversville, June 24 (C. P. A.).
Herkimer County: Indian Castle, June 13 (C. P. A.).
Tompkins County: Ithaca, May 3 to June 20 (C. P. A.); Ludlowville, May 4 (E. M.).
Wyoming County: Portage, May 24 (H. H. K.).
T. latipennis Loew
Erie County: Buffalo, June 26 (M. C. VD.); Grand Island, June 26 (M. C. VD.).
Fulton County: Sacandaga Park, July 3 (C. P. A.).
Genesee County: Batavia, August 1 (H. H. K.).
Niagara County: Grand Island, June 26 (M. C. VD.).
Rensselaer County: Brookview, July 15 (M. M. A.).
T. longiventris Loew
Cattaraugus County: Rock City, June 6 (W. T. M. F.).
Erie County: East Auburn, June 11 (M. C. VD.).
Fulton County: Sacandaga Park, July 29 (C. P. A.); Woodworth's Lake, August (C. P. A.).
Suffolk County: Bellport, May 27, July 6. (Part of the type material was collected in New York State by Edwards.)
T. macrolabis Loew
Albany County: Helderbergs, July 3 (C. P. A.).
Fulton County: Mount Buell, June 18–27 (C. P. A.); etc.
Herkimer County: Indian Castle, June 13 (C. P. A.).
T. margarita Alex.
Tompkins County: Ithaca, June 12 (C. P. A.), T. L.
T. mingwe Alex.
Fulton County: Sacandaga Park, August 24 (C. P. A.).
Genesee County: Batavia, July 22 (H. H. K.).
Hamilton County: Bennett Lake, Hope Township, September 12 (C. P. A.), T. L.
Onondaga County: Manlius, August 20 (H. H. S.).
Schoharie County: Sharon Springs (O. S.).
Tompkins County: Ithaca, August 1 (C. P. A.).
Wayne County: Sodus, July 9.
T. monticola Alex.
Cattaraugus County: Rock City, June 16 (H. H. K.).
Fulton County: Woodworth's Lake, June 18 (C. P. A.), T. L.; etc.
Hamilton County: Wells, July 23 (D. B. Y.).
Herkimer County: Indian Castle, June 13 (C. P. A.).
Tompkins County: Ithaca, June 3 (S. A. G.); McLean, June 5 (C. P. A.).
T. nobilis (Loew)
Albany County: Karner, June 19 (D. B. Y.).
Fulton County: Sacandaga Park, June 17 (C. P. A.); Woodworth's Lake, June 23 (C. P. A.).
Tompkins County: McLean, June 5 (C. P. A.).
Wyoming County: June 25 (H. H. K.).

Genus *Tipula* Linnaeus (*continued*)

Subgenus *Tipula* Linnaeus (*continued*)

T. parshleyi Alex.

Franklin County: Axton, June 12–22 (A. D. M. and C. O. H.).

T. penobscot Alex.

Fulton County: Mount Buell, altitude 1800 feet, June 18 (C. P. A.).

T. perlongipes Johns.

Fulton County: Canada Lake, altitude 1500 feet, June 20 (C. P. A.).
Queens County: Flushing, June 22 (C. R. P.).

T. rohweri Doane

Erie County: East Aurora, May 18 (M. C. VD.); Elma, August 20 (M. C. VD.).

(Mr. Van Duzee records this species, but the record seems very doubtful to the writer since typical *rohweri* is western in its distribution.)

T. sackeniana Alex.

Tompkins County: Ithaca, August 26 (C. P. A.), T. L.

T. sayi Alex.

Cattaraugus County: Olean, September 5 (C. R. C.).
Cayuga County: North Fair Haven, September 12 (C. P. A.).
Erie County: Elma, August 20 (M. C. VD.); Hamburg, September 11–25 (M. C. VD.); Buffalo, September 21 (M. C. VD.); etc.
Fulton County: Gloversville, September 17–25 (C. P. A.); etc.
Genesee County: Batavia, September 11 (H. H. K.).
Herkimer County: Old Forge, August 23 (J. G. N.).
New York: August 5 to September 23.
Orange County: Goshen, September 7; West Point, September 8 (O. S.).
Sullivan County: August (Dietz collection).
Tompkins County: Ithaca, August 26–28 (C. P. A.); etc.
Warren County: County-Line Flow, Griffin, July 26 (C. P. A.).

T. senega Alex.

Albany County: Helderbergs, June 12 (C. P. A.).
Erie County: Holland, May 21 (M. C. VD.); East Aurora, June 11 (M. C. VD.).
Fulton County: Mountain Lake, June 13–23 (C. P. A.); Mount Buell, June 15–29 (C. P. A.).
Tompkins County: Ithaca, May 7 to June 20 (L. W. C.); McLean, June 5 (C. P. A.).

T. serta Loew

Erie County: Holland, May 21 (M. C. VD.); Lancaster, May 31 (M. C. VD.); Buffalo, June 5 (M. C. VD.).
Fulton County: Gloversville, June 6–20 (C. P. A.); etc.
Tompkins County: Ithaca, May 31 to June 20 (C. P. A.); etc.

T. strepens Loew

Cortland County: Taylor, July 20 (C. P. A.); Cincinnatus, July 21 (C. P. A.).
Fulton County: Sacandaga Park, June 6–20 (C. P. A.); etc.
Herkimer County: Indian Castle, June 13 (C. P. A.).
Niagara County: Niagara Falls, June 24 (M. C. VD.).
Rockland County: Palisades (O. S.).
Saratoga County: Corinth, June 22 (D. B. Y.).
Tioga County: Willseyville, May 25 (W. A. H.).
Tompkins County: Ithaca, May 20–29 (C. P. A.); McLean, June 5 (C. P. A.).

T. submaculata Loew

Albany County: Albany, June 26 (D. B. Y.); Helderbergs, July 3 (C. P. A.).
Cattaraugus County: Four-Mile, July 4 (H. H. K.).

Genus *Tipula* Linnaeus (*continued*)
Subgenus *Tipula* Linnaeus (*continued*)
T. submaculata Loew (*continued*)
Cortland County: Cincinnatus, July 21 (C. P. A.).
Erie County: North Evans, July 4 (M. C. VD.).
Fulton County: Sacandaga Park, June 20 to July 4 (C. P. A.); Gloversville, June 27 (C. P. A.); etc.
Genesee County: Batavia, July 14–25 (H. H. K.).
Saratoga County: Corinth, June 23 (D. B. Y.).
Tompkins County: Ithaca, June 20 (L. W. C.); etc.
(Part of the type material was collected in New York State.)
T. sulphurea Doane
Onondaga County: Green Lake, June 8 (C. P. A.).
T. taughannock Alex.
Albany County: Helderbergs, June 12 (C. P. A.).
Fulton County: Mount Buell, altitude 1800 feet, June 13 (W. P. A. and C. P. A.), T. L.
Tompkins County: Taughannock Falls, May 19 (C. P. A.).
T. tephrocephala Loew
Albany County: Karner, June 5 (D. B. Y.).
Fulton County: Sacandaga Park, June 16–28 (C. P. A.); etc.
Genesee County: Batavia, June 1 (H. H. K.).
Herkimer County: Indian Castle, June 9 (C. P. A.).
Rockland County: Palisades (O. S.), T. L.
Schenectady County: Schenectady, June 14 (C. P. A.).
Tompkins County: Ithaca, May 16–29 (C. P. A.); McLean, June 5 (C. P. A.).
T. tricolor Fabr.
Columbia County: Niverville, August 24 (A. P. M.).
Cortland County: Cincinnatus, July 21 (C. P. A.).
Fulton County: Gloversville, August 18 to September 12 (C. P. A.); etc.
Genesee County: Batavia, June 19 (H. H. K.).
Herkimer County: Indian Castle, June 9–13 (C. P. A.); Trenton Falls, July (O. S.).
New York: (Hy. Edwards collection.)
Suffolk County: July.
Tompkins County: Ithaca, May 29 to August 28 (C. P. A.); etc.
T. trivittata Say
Albany County: Albany, June 11 (D. B. Y.); Helderbergs, June 12 (C. P. A.).
Cattaraugus County: Mix Creek Valley, June 11 (J. C. B.).
Cortland County: Blodgett Mills, June 29 (A. O.).
Erie County: Lancaster, May 31 to June 2 (M. C. VD.); South Wales, July 9 (M. C. VD.); etc.
Fulton County: Sacandaga Park, June 11 (C. P. A.); etc.
Genesee County: Batavia, June 22–23 (H. H. K.).
Niagara County: Niagara Falls, June 24 (M. C. VD.).
Schenectady County: Schenectady, June 14 (C. P. A.).
Tompkins County: Ithaca, May 17 to July 2 (C. P. A.); etc.
T. ultima Alex.
Cayuga County: North Fair Haven, September 12 (C. P. A.).
Delaware County: Delhi, September 21 (A. M.).
Erie County: Hamburg, September 11–25 (M. C. VD.); Lancaster, September 13 (M. C. VD.); etc.
Fulton County: Gloversville, September 15–20 (C. P. A.); etc.
Genesee County: Batavia, September 12–28 (H. H. K.).
Hamilton County: Middle Lake, Hope Township, September 13 (C. P. A.).

Genus *Tipula* Linnaeus (*continued*)
Subgenus *Tipula* Linnaeus (*continued*)
T. ultima Alex. (*continued*)
Kings County: Flatbush, September 28.
Suffolk County: North Beach, September 18.
Tompkins County: Ithaca, September 29 to October 10 (C. P. A.).
Westchester County: Peekskill, September 15 (Van Atta).
T. umbrosa Loew
Essex County: Keene Valley, August 10 (J. A. L.).
Fulton County: Sacandaga Park, June 24–29 (C. P. A.).
Hamilton County: Long Lake, August 9 (J. A. L.).
Herkimer County: Old Forge, July 25 (J. G. N.).
Tompkins County: Ithaca, July 20 (L. W. C.).
T. valida Loew
Albany County: Helderbergs, June 12 (C. P. A.).
Cattaraugus County: Rock City, June 16 (H. H. K.).
Erie County: Lancaster, June 2–4 (M. C. VD.); North Evans, July 4 (M. C. VD.); etc.
Fulton County: Woodworth's Lake, May 30 to June 15 (C. P. A.); Sacandaga Park, June 1–21 (C. P. A.).
Herkimer County: Indian Castle, June 13 (C. P. A.).
Onondaga County: Green Lake, June 8 (C. P. A.).
Saratoga County: Corinth, June 22 (D. B. Y.).
Tompkins County: Ithaca, May 26 to June 20 (C. P. A.).
T. vicina Dietz
Erie County: Lancaster, May 31 (M. C. VD.), T. L.; Hamburg, June 7 (M. C. VD.).

Regional species: *Aeshnasoma rivertonensis* Johns., *Nephrotoma approximata* (Dietz), *N. cingulata* (Dietz), *N. festina* (Dietz), *N. hirsutula* (Dietz), *N. obliterata* (Dietz), *N. occipitalis* (Loew), *N. penumbra* Alex., *N. punctum* (Loew), *N. stigmatica* (Dietz), *N. temeraria* (Dietz), *N. vittula* (Loew), *N. wyalusingensis* (Dietz), *Tipula angulata* Loew, *T. annulicornis* Say, *T. aprilina* Alex., *T. centralis* Loew, *T. cincticornis* Doane, *T. conspicua* Dietz, *T. fraterna* Loew, *T. huron* Alex., *T. johnsoniana* Alex., *T. mainensis* Alex., *T. megaura* Doane, *T. morrisoni* Alex., *T. pachyrhinoides* Alex., *T. ternaria* Loew.

Distribution of the Tipulidae and related families by life zones

North America may be divided into seven roughly parallel belts, or zones, termed life zones, which extend more or less completely across the continent and are distinguished from one another by peculiarities of their fauna and flora, by the annual precipitation, and by other characteristics. Beginning with the treeless Arctic-Alpine zone in northern Canada and passing southward, they comprise the Hudsonian, the Canadian, the Transition, the Upper Austral, the Lower Austral, and finally the Tropical zone, the last-named being found in the United States only in southern Florida and Texas.

These belts are by no means regularly parallel. In certain localities they run north or south at right angles to their usual course and encroach

on the adjacent zones. Thus the Canadian life zone of southern Canada and the northern United States extends southward in the mountains as far as Georgia, the same faunal and floral conditions prevailing in the high Alleghenies of Virginia and the Great Smoky Mountains of western North Carolina as are found at much lower levels in the northern parts of the United States. By this it is seen that the same result is obtained by climbing these mountains as by a long journey from south to north, a rise of a few feet in altitude being equivalent to many miles of latitude. Similarly there are extensions of the Upper Austral zone northward into the Transition zone, these being produced by favorable conditions of warmth and moisture. In New York State is found an extensive Austral belt along the southern shores of Lake Ontario, altho the country due southward is Transitional or even Canadian in its tendencies. Such isolated islands are by no means infrequent.[4]

The crane-fly fauna seems to be fairly well distributed in these zones, and in the following pages the various species are arranged in their respective places. As has already been stated, crane-flies are notable lovers of rich vegetation, usually near running or standing water. Definite groups of crane-fly species may be expected to occur in certain floral communities, this relationship being often well marked. In cold Canadian woods, such as are found in the Adirondacks and Catskills and as isolated islands in the bogs and gorges thruout the State, definite plant associations are found, each of which supports an equally well-defined society of crane-flies. As a correlation and aid in checking these various species, the plants that the writer believes to be characteristic of the different life zones are herewith included.

The Boreal region

The Arctic-Alpine zone.— "The Arctic or Arctic-Alpine zone lies above the limit of tree growth and is characterized by such plants as the arctic poppy, dwarf willow, and various saxifrages and gentians. . . .

[4] The following papers refer to this subject:
Bray, William L. The development of the vegetation of New York State. New York State Coll. Forestry, Syracuse Univ., Tech. pub. 3:1-186. 1915.
Eaton, Elon Howard. Life zones of New York State. *In* Birds of New York. New York State Museum, Memoir 12[1]:19-42. 1910.
Merriam, C. Hart. The geographic distribution of life in North America. Smithsonian Inst., Ann. Rept. Bd. Regents **1891**: 365-415. 1893.
Merriam, C. Hart. Life zones and crop zones of the United States, Part II. U. S. Dept. Agr., Div. Biol. Survey, Bul. 10 : 18-53. 1898.
Miller, Gerrit S., jr. Life zones of New York. *In* Preliminary list of the mammals of New York. New York State Museum, Bul. 6[29] : 280-292. 1899.

Within the United States the Arctic-Alpine zone is restricted to the area above timber-line on the summits of high mountains." (Merriam, 1898: 18–19.)

The crane-flies in this zone are considered in connection with those in the Hudsonian zone.

The Hudsonian zone.— "The Hudsonian zone comprises the northern part of the great transcontinental coniferous forest — a forest of spruces and firs stretching from Labrador to Alaska — and . . . In the eastern United States the Hudsonian zone is restricted to the cold summits of the highest mountains, where it occurs in the form of a chain of widely separated islands reaching from northern New England to western North Carolina." (Merriam, 1898: 19.)

The following plants may be considered as Hudsonian species:

Hierochloë alpina (Sw.) R. & S.
Poa laxa Haenke
Scirpus caespitosus L.
Carex capillaris L.
rariflora Smith
rigida Good.
capitata L.
Juncus trifidus L.
Salix herbacea L.
Uva-ursi Pursh
Betula glandulosa Michx.
Arenaria groenlandica (Retz.) Spreng.
Saxifraga aizoides L.
Ranunculus lapponicus L.
Empetrum nigrum L.
Rhododendron lapponicum (L.) Wahlenb.
Cassiope hypnoides (L.) D. Don.
Arctostaphylos alpina (L.) Spreng.
Vaccinium caespitosum Michx.
uliginosum L.
Vitis-Idaea L., var. *minus* Lodd.
Diapensia lapponica L.
Primula mistassinica Michx.
Pinguicula vulgaris L.
Prenanthes nana (Bigel.) Torr.
Solidago Cutleri Fernald

The following species of crane-flies may be considered as Arctic-Alpine species finding their southern limit in the Hudsonian zone:

Rhabdomastix caudata (Lundb.)
Tricyphona hannai Alex.
hyperborea (O. S.)
Tipula aperta Alex.
appendiculata Loew
arctica Curt.
*baliopter*a Loew
besselsi O. S.
canadensis Loew
Tipula centralis Loew
labradorica Alex.
loewiana Alex.
piliceps Alex.
septentrionalis Loew
serrulata Loew
subfasciata Loew
ternaria Loew

The Canadian zone.— "The Canadian zone comprises the southern part of the great transcontinental coniferous forest of Canada, the northern parts of Maine, New Hampshire, and Michigan, . . . and the greater part of the high mountains of the United States and Mexico." (Merriam, 1898: 19.)

The following plants may be considered as Canadian species:

Carex exilis Dewey
tenuiflora Wahlenb.
diandra Schrank
pauciflora Lightf.
leptalea Wahlenb.
livida (Wahlenb.) Willd.
oligosperma Michx.
Calla palustris L.
Clintonia borealis (Ait.) Raf.
Smilacina trifolia (L.) Desf.
Streptopus amplexifolius (L.) DC.
Trillium undulatum Willd.
Habenaria macrophylla Goldie
bracteata (Willd.) R. Br.
Arethusa bulbosa L.
Calypso bulbosa (L.) Oakes
Salix rostrata Richards
candida Flügge
Populus balsamifera L.
Betula alba var. *papyrifera* (Marsh.) Spach.
Stellaria borealis Bigel.
Coptis trifolia (L.) Salisb.
Actaea rubra (Ait.) Willd.
Mitella nuda L.
Ribes triste Pall.
Pyrus americana (Marsh.) DC.
Potentilla tridentata Ait.
Dalibarda repens L.
Oxalis Acetosella L.
Ilex monticola Gray
Acer spicatum Lam.
Rhamnus alnifolia L'Hér.
Viola Selkirkii Pursh
lanceolata L.
Epilobium molle Torr.
Circaea alpina L.
Panax quinquefolium L.
Cornus canadensis L.
Ledum groenlandicum Oeder
Kalmia polifolia Wang.
Andromeda glaucophylla Link.
Chamaedaphne calyculata (L.) Moench
Arctostaphylos Uva-ursi (L.) Spreng.
Chiogenes hispidula (L.) T. & G.
Menyanthes trifoliata L.
Galium labradoricum Wiegand
Lonicera oblongifolia (Goldie) Hook.
Linnaea borealis L., var. *americana* (Forbes) Rehder
Viburnum alnifolium Marsh.
Solidago macrophylla Pursh
uliginosa Nutt.
Senecio Robbinsii Oakes

The following species of crane-flies may be considered as Canadian species:

Bittacomorphella jonesi (Johns.)
Dicranomyia halterata O. S.
Limnobia hudsonica O. S.
parietina O. S.
solitaria O. S.
tristigma O. S.
Dicranoptycha germana O. S.
Toxorhina muliebris (O. S.)
Erioptera chrysocoma O. S.
megophthalma Alex.
nyctops Alex.
stigmatica (O. S.)
straminea O. S.
Ormosia monticola (O. S.)
pygmaea (Alex.)
Adelphomyia cayuga Alex.
minuta Alex.
Limnophila alleni Johns.
johnsoni Alex.
munda O. S.
osborni Alex.
stanwoodae Alex.
subcostata (Alex.)
subtenuicornis (Alex.)
Limnophila tenuicornis O. S.
toxoneura O. S.
unica O. S.
Eriocera brachycera O. S.
Rhaphidolabis flaveola O. S.
modesta (O. S.)
rubescens Alex.
Dicranota pallida Alex.
Tricyphona auripennis (O. S.)
calcar (O. S.)
katahdin Alex.
Cylindrotoma americana O. S.
tarsalis Johns.
Phalacrocera neoxena Alex.
tipulina O. S.
Nephrotoma penumbra Alex.
vittula (Loew)
Tipula angulata Loew
cayuga Alex.
macrolabis Loew
mainensis Alex.
monticola Alex.
penobscot Alex.
serta Loew

The Canadian-Transition zone.— A great many species occur in both the Canadian and the Transition life zone, and these for the most part find their northern or southern limit in one or the other of these belts. The floral constituents of this border zone are numerous and varied, a large number of the Canadian forms finding their southern limit in the Transition zone, and, conversely, many of the more southern species extending their range into, and finding their northern limit in favorable situations in, the Canadian zone. The more notable plants that seem to fall within this category are:

Maianthemum canadense Desf.
Streptopus roseus Michx.
Medeola virginiana L.
Cypripedium arietinum R. Br.
    hirsutum Mill.
Habenaria lacera (Michx.) R. Br
Laportea canadensis (L.) Gaud.
Arceuthobium pusillum Peck
Asarum canadense L.
Polygonum amphibium L.
Caltha palustris L.
Actaea alba (L.) Mill.
Caulophyllum thalictroides (L.) Michx.
Corydalis sempervirens (L.) Pers.
Pyrus arbutifolia (L.) L. f.
    melanocarpa (Michx.) Willd.
Potentilla palustris (L.) Scop.
Rubus hispidus L.
Sanguisorba canadensis L.
Nemopanthus mucronata (L.) Trel.
Acer pennsylvanicum L.
Hypericum canadense L.
Trientalis americana (Pers.) Pursh
Gentiana linearis Froel.
Diervilla Lonicera Mill.
Viburnum cassinoides L.
Lobelia Kalmii L.
Solidago latifolia L.
    rugosa Mill.
    graminifolia (L.) Salisb.
Aster umbellatus Mill.
Anaphalis margaritacea (L.) B. & H.
Erechtites hieracifolia (L.) Raf.

The majority of the crane-flies of the northeastern United States seem to belong here. There are many species which are strongly Canadian in their associations but still seem to range outside the Canadian zone. In the following list these species are designated by the letter *C*, in parenthesis. It must be understood that many of these species are about as typically Canadian as those given in the preceding list, but slight extensions of their range make it appear more desirable to include them in this qualified list.

The few species which are Transitional but range into the Canadian zone are here designated by the letter *T*.

Protoplasa fitchii O. S.
Trichocera subsinuata Alex. (C)
Rhyphus alternatus Say
Dicranomyia gladiator O. S. (C)
    globithorax O. S. (C)
    haeretica O. S.
    immodesta O. S.
Dicranomyia macateei Alex. (C)
    monticola (Alex.) (C)
    morioides O. S.
    pubipennis O. S. (C)
    pudica O. S.
Limnobia triocellata O. S.
Rhipidia fidelis O. S.

Rhipidia maculata Meig.
Atarba picticornis O. S.
Elephantomyia westwoodi O. S. (C)
Rhamphidia mainensis Alex.
Ormosia apicalis Alex. (C)
holotricha (O. S.)
innocens (O. S.)
meigenii (O. S.)
nigripila (O. S.)
nubila (O. S.)
rubella (O. S.)
Erioptera armata O. S.
armillaris O. S.
villosa O. S. (C)
Molophilus fultonensis Alex. (C)
hirtipennis (O. S.)
pubipennis (O. S.)
ursinus (O. S.)
Gnophomyia tristissima O. S.
Gonomyia alexanderi (Johns.)
blanda O. S. (C)
cognatella O. S. (T)
florens Alex. (C)
mathesoni Alex.
noveboracensis Alex. (T)
sacandaga Alex. (T)
subcinerea O. S.
sulphurella O. S. (T)
Rhabdomastix flava (Alex.) (T)
Cryptolabis paradoxa O. S.
Chionea valga Harr.
Cladura delicatula Alex. (C)
flavoferruginea O. S.
Adelphomyia americana Alex. (C)
Limnophila albipes Leon. (C)
aprilina O. S. (C)
areolata O. S. (C)
brevifurca O. S. (C)
edwardi Alex. (C)
emmelina Alex. (C)
fuscovaria O. S. (C)
imbecilla O. S.
inornata O. S.
laricicola Alex. (C)
lenta O. S.
montana O. S.
mundoides Alex.
nigripleura A. & L. (C)
niveitarsis O. S. (C)
noveboracensis Alex. (C)
quadrata O. S.
rufibasis O. S. (C)
sylvia Alex. (C)
ultima O. S. (C)
Ula elegans O. S. (C)
Ulomorpha pilosella (O. S.) (C)
Eriocera fultonensis Alex.
longicornis (Walk.)
spinosa (O. S.)
tristis Alex.
Hexatoma megacera (O. S.)
Dicranota eucera O. S.
noveboracensis Alex.
rivularis O. S.
Rhaphidolabis cayuga Alex.
tenuipes O. S.
Pedicia albivitta Walk.
contermina Walk. (C)
Tricyphona paludicola Alex.
vernalis (O. S.) (C)
Liogma nodicornis (O. S.) (C)
Triogma exculpta O. S.
Dolichopeza americana Needm. (C)
Oropeza albipes Johns.
obscura Johns. (C)
venosa Johns. (C)
Ctenophora apicata O. S.
Nephrotoma eucera (Loew)
incurva (Loew)
lugens (Loew) (C)
pedunculata (Loew) (C)
polymera (Loew)
tenuis (Loew)
xanthostigma (Loew)
Stygeropis fuscipennis Loew
Longurio testaceus Loew (C)
Tipula algonquin Alex.
angustipennis Loew (C)
apicalis Loew (C)
bicornis Forbes
caloptera Loew
collaris Say (C)
cunctans Say (T)
dejecta Walk. (C)
fragilis Loew (C)
fuliginosa (Say) (T)
hebes Loew (C)
hermannia Alex. (C)
hirsuta Doane
iroquois Alex. (C)
latipennis Loew (C)
longiventris Loew
megaura Doane (C)
mingwe Alex.
nobilis (Loew) (C)
oropezoides Johns. (C)
parshleyi Alex. (C)
perlongipes Johns. (T)
senega Alex.

Tipula strepens Loew
submaculata Loew
sulphurea Doane (C)
taughannock Alex. (C)
Tipula tephrocephala Loew
ultima Alex. (T)
unimaculata (Loew)
valida Loew (C)

The Austral region

The Transition zone.—"The Transition zone . . . is the transcontinental belt in which Boreal and Austral elements overlap. From New England to the northern Rocky Mountains its course is fairly even and regular." (Merriam, 1898:20.)

The following plants may be considered as Transition species:

Schizaea pusilla Pursh
Chamaecyparis thyoides (L.) BSP.
Trillium grandiflorum (Michx.) Salisb.
cernuum L.
Aletris farinosa L.
Smilax hispida Muhl.
Juglans nigra L.
Ulmus racemosa Thomas
Sassafras variifolium (Salisb.) Ktze.
Crotalaria sagittalis L.
Polygala Nuttallii T. & G.
Nyssa aquatica L.
Asclepias verticillata L.
Datura Stramonium L.
Pentstemon hirsutus (L.) Willd.
Dianthera americana L.

The crane-flies of this area include the following species:

Dicranomyia rara O. S.
Limnobia fallax Johns.
Dicranoptycha sobrina O. S.
Gonomyia manca (O. S.)
Limnophila cubitalis O. S.
fasciolata O. S.
irrorata Johns.
Aeshnasoma rivertonensis Johns.
Tipula annulicornis Say
eluta Loew
fraterna Loew
georgiana Alex.
sayi Alex.
tricolor Fabr.
tuscarora Alex.
umbrosa Loew

Limnophila cubitalis perhaps might be better included in the list preceding this. *Tipula umbrosa* ranges from the Austral to the Canadian zone, but seems most numerous in the Transition zone.

The Upper Austral zone.—"The Carolinian faunal area [of the Upper Austral zone] . . . . occupies the larger part of the Middle States, except the mountains." (Merriam, 1898:30.)

The following plants may be considered as Upper Austral species:

Pinus virginiana Mill.
echinata Mill.
Commelina communis L.
Saururus cernuus L.
Quercus falcata Michx.
marilandica Muench.
phellos L.
Nelumbo lutea (Willd.) Pers.
Cabomba caroliniana Gray
Asimina triloba Dunal
Corydalis flavula (Raf.) DC.
Liquidambar Styraciflua L.
Desmodium laevigatum (Nutt.) DC.
Lespedeza repens (L.) Bart.
Ptelea trifoliata L.[5]
Evonymus americanus L.

[5] Species characteristic of this zone but running into the Transition zone.

Ascyrum stans Michx.
Aralia spinosa L.
Ipomoea pandurata (L.) G. F. W. Mey.
Paulownia tomentosa (Thunb.) Steud.
Lonicera sempervirens L.
Viburnum nudum L.

The following species of crane-flies belong to this zone:

Dicranoptycha minima Alex.
nigripes O. S.
tigrina Alex.
winnemana Alex.
Toxorhina magna (O. S.)[6]
Gnophomyia luctuosa O. S.[6]
Epiphragma solatrix (O. S.)
Eriocera aurata Doane
wilsonii O. S.
Brachypremna dispellens (Walk.)[6]
Nephrotoma okefenoke (Alex.)
virescens (Loew)[7]
Tipula australis Doane
dietziana Alex.
flavibasis Alex.
morrisoni Alex.

The Lower Austral zone.—"The Lower Austral zone occupies the southern part of the United States, from Chesapeake Bay to the great interior valley of California." (Merriam, 1898:41.)

This is a region characterized by a great number of southern plants, of which the cabbage palmetto (*Sabal palmetto* Lodd.), the Venus's fly-trap (*Dionaea muscipula* Ellis), and the crape myrtle (*Lagerstroemia indica* L.) may be cited as typical. The following species of crane-flies belong to this zone:

Dicranomyia distans O. S.
floridana O. S.
Diotrepha mirabilis O. S.[8]
Gonomyia pleuralis (Will.)[8]
puer Alex.[8]
slossonae Alex.[8]
Polymera georgiae Alex.
Tipula aspidoptera Alex.
comanche Alex.
costaloides Alex.
guasa Alex.
ludoviciana Alex.
seminole Alex.
texensis Alex.

The Tropical region

The Tropical zone.— "The Tropical region within the United States is of small extent and is restricted to three widely separated localities — southern Florida, extreme southeast Texas . . . , and the valley of the lower Colorado River in Arizona and California. The Florida area is genuine humid tropical." (Merriam, 1898:51–52.)

The following species of crane-flies pertain to this zone:

Dicranomyia reticulata Alex.
Rhipidia schwarzi Alex.
Geranomyia virescens Loew
Erioptera immaculata Alex.
Megistocera longipennis (Macq.)

[6] Southern species reaching their northern limit in this zone.
[7] Species characteristic of this zone but running into the Transition zone.
[8] Tropical species reaching their northern limit in this zone.

SEASONAL DISTRIBUTION

Like many other groups of insects, the Holarctic crane-flies have a remarkably constant seasonal distribution, there being vernal, early summer, midsummer, and autumnal species, as well as forms that range over a much longer period. The vernal species appear soon after the melting of the ice in spring, and are on the wing for a month or two. Some few of these species reappear in late summer, and these are presumably double-brooded species. In New York, New England, and southern Canada the great majority of crane-flies are on the wing during the month of June. Among these are represented the last of the vernal forms and the first of the extensive midsummer fauna. In late summer a few additional species appear, and these are closely followed in September and October by about the same number of autumnal forms. The winter crane-flies, so-called, include species of Trichocera and Chionea which appear at other seasons of the year as well but are more easily detected during the mild, sunny days of winter.

In general it may be stated that the crane-flies of eastern America which fly in spring and summer come out later and disappear earlier in the northern part of their range — New York, New England, and southern Canada — than in the southern part — the Middle Atlantic and Southern States. The late summer and the autumnal species, however, come out earlier in the former regions than they do farther south, and disappear correspondingly early in the season, their period being restricted by the date of the first killing frost.

The dates as here given apply to the Transition areas of New York and New England. They should be considered as earlier in the vicinity of Washington — from one to three weeks or even more, depending on the situation — and later as one goes northward, with the exceptions given above. It must be understood and expected that considerable deviation from these dates and figures will be found, but it is believed that in most cases they are fairly accurate, being based on a vast number of records extending over many years.

The following are early to late spring species — from April 1 thru May, disappearing about the first of June but many of them reappearing in August and September. Most of these species appear for the first time about April 20. Helobia appears much earlier, in March or even in February. The species of Ormosia, Dicranota, and Rhaphidolabis are

especially characteristic of the early spring fauna, appearing in small swarms soon after the breaking up of the winter's snow and ice. Practically all the species have disappeared by June 1, but *Tipula trivittata* is found thruout the summer.

Ormosia innocens (O. S.)
meigenii (O. S.)
nubila (O. S.)
Helobia hybrida (Meig.)
Limnophila subcostata (Alex.)
Dicranota eucera O. S.
noveboracensis Alex.
rivularis O. S.
Rhaphidolabis cayuga Alex.
Rhaphidolabis tenuipes O. S.
Pedicia contermina Walk.
Tricyphona paludicola Alex.
Tipula angustipennis Loew
collaris Say
dejecta Walk.
iroquois Alex.
tephrocephala Loew
trivittata Say

In Europe the following species appear to be characteristic early spring forms:

Tipula macrocera Zett.
maxima Poda
pabulina Meig.
Tipula variipennis Meig.
vittata Meig.

Late spring to midsummer species — June, some persisting into July and a few reappearing in late summer — are as follows. *Limnophila brevifurca* appears in early May but is not common until June. It will be seen from this list that the majority of the local Limnophilas appear in the month of June.

Protoplasa fitchii O. S.
Toxorhina muliebris (O. S.)
Dicranoptycha germana O. S.
Atarba picticornis O. S.
Rhamphidia mainensis Alex.
Erioptera nyctops Alex.
vespertina O. S.
Gnophomyia tristissima O. S.
Gonomyia florens Alex.
mathesoni Alex.
noveboracensis Alex.
subcinerea O. S.
sulphurella O. S.
Limnophila alleni Johns.
aprilina O. S.
areolata O. S.
brevifurca O. S.
cubitalis O. S.
edwardi Alex.
emmelina Alex.
fasciolata O. S.
fuscovaria O. S.
Limnophila johnsoni Alex.
munda O. S.
niveitarsis O. S.
poetica O. S.
quadrata O. S.
rufibasis O. S.
sylvia Alex.
tenuicornis O. S.
toxoneura O. S.
unica O. S.
Adelphomyia minuta Alex.
Ulomorpha pilosella (O. S.)
Hexatoma megacera (O. S.)
Eriocera cinerea Alex.
longicornis (Walk.)
spinosa (O. S.)
Tricyphona auripennis (O. S.)
calcar (O. S.)
vernalis (O. S.)
Rhaphidolabis flaveola O. S.
modesta (O. S.)
rubescens Alex.

Liogma nodicornis (O. S.)
Dolichopeza americana Needm.
Nephrotoma lugens (Loew)
Tipula apicalis Loew
cayuga Alex.
macrolabis Loew
monticola Alex.
Tipula oropezoides Johns.
penobscot Alex.
senega Alex.
serta Loew
submaculata Loew
sulphurea Doane
taughannock Alex.

Early summer to midsummer species — from June 21 to August 10 — are as follows:

Bittacomorphella jonesi (Johns.)
Dicranomyia globithorax O. S.
macateei Alex.
pubipennis O. S.
Limnobia triocellata O. S.
tristigma O. S.
Elephantomyia westwoodi O. S.
Ormosia monticola (O. S.)
nigripila (O. S.)
rubella (O. S.)
Erioptera armillaris O. S.
chlorophylla O. S.
chrysocoma O. S.
graphica O. S.
straminea O. S.
Molophilus fultonensis Alex.
hirtipennis (O. S.)
pubipennis (O. S.)
ursinus (O. S.)
Gonomyia alexanderi (Johns.)
blanda O. S.
manca (O. S.)
sacandaga Alex.
Rhabdomastix flava (Alex.)
Cryptolabis paradoxa O. S.
Limnophila albipes Leon.
inornata O. S.
nigripleura A. & L.
noveboracensis Alex.
stanwoodae Alex.
Penthoptera albitarsis O. S.
Eriocera fultonensis Alex.
tristis Alex.
Cylindrotoma americana O. S.
tarsalis Johns.
Phalacrocera neoxena Alex.
tipulina O. S.
Longurio testaceus Loew
Nephrotoma eucera (Loew)
xanthostigma (Loew)
Tipula fuliginosa (Say)
hebes Loew
hermannia Alex.
tricolor Fabr.
valida Loew

In Europe the following species seem to have this seasonal distribution:

Tipula cava Ried.
livida v. d. W.
Tipula trifasciata Loew
vernalis Meig.

Midsummer to late summer species — from August 10 to September 10 — are as follows:

Dicranomyia longipennis (Schum.)
Limnobia solitaria O. S.
Erioptera parva O. S.
Adelphomyia americana Alex.
cayuga Alex.
Tricyphona autumnalis Alex.
katahdin Alex.
Tipula abdominalis (Say)
sayi Alex.
unimaculata (Loew)

In Europe the following species seem to have this seasonal distribution:

Tipula bifasciculata Loew
dilatata Schum.
Tipula fulvipennis DeG.
helvola Loew

Autumnal species — from September 10 to snowfall — are as follows. *Limnophila ultima* is sometimes vernal but is commoner in late summer and autumn. *Discobola argus* is found at other seasons but is more numerous in September. *Cladura flavoferruginea, Limnophila ultima*, and *Tipula cunctans* have a longer flight-period than most of the others listed.

Dicranomyia brevivena O. S.
Limnobia parietina O. S.
Discobola argus (Say)
Cladura delicatula Alex.
flavoferruginea O. S.
Limnophila osborni Alex.
ultima O. S.
Tricyphona autumnalis Alex.
Tipula cunctans Say
fragilis Loew
ultima Alex.
unifasciata (Loew)

The following European species seem to have this seasonal distribution:

Tipula anonyma Bergr.
autumnalis Loew
interserta Ried.
luteipennis Meig.
marmorata Meig.
Tipula melanoceros Schum.
obsoleta Meig.
pagana Meig.
rufina Meig.
signata Staeg.

IMMATURE STAGES

THE EGG

The egg stage is generally of short duration, usually lasting from one to three weeks. In *Tipula sayi* it is eight days. The number of eggs laid, so far as is known, ranges from about forty-five in *Styringomyia didyma* to about two thousand in the larger species of Eriocera. The eggs are deposited in different ways according to the species, the details of which are discussed elsewhere (page 881).

The eggs are without an intricate sculpturing, but may be finely punctured or striate. They are black, with a heavy chorion in the Tipulinae and in the tribe Hexatomini. In most of the Limnobiinae and the Cylindrotominae they are white and pellucid, or even a light orange-red in some cases, as in the genus Dicranomyia.

THE LARVA

The larval, or feeding, stage is the longest in the life of a crane-fly, in the known cases requiring the greater part of the year. Some of the smaller forms are presumably double-brooded, since they appear in the spring, are absent during most of the summer, and reappear in the late

summer and early fall. In such cases the larval existence is, of course, greatly shortened. The larval habitat is exceedingly varied and may be summarized as follows:[9]

Tanyderidae.— Nothing whatever is known of the immature stages of this group of flies, and it is very desirable that some of the forms should be reared. They are very rare, however, and even the adults are uncommon in collections. It is very probable that the larvae of species of Protoplasa, the only genus in the Northern Hemisphere, will be found to be amphibious, such a larval habitat often characterizing primitive forms.

Ptychopteridae.— Semi-aquatic or amphibious (Ptychoptera, Bittacomorpha, Bittacomorphella).

Rhyphidae.—In decaying vegetable and animal matter (Trichocera, Mycetobia, Rhyphus).

Tipulidae.— Limnobiini: Aquatic, in silken cases or tubes among submerged mosses (*Dicranomyia simulans*); semi-aquatic or in moist earth (*Limnobia fallax*, and probably *L. solitaria* and *L. parietina*); in decaying vegetable matter (*Limnobia indigena, Rhipidia domestica*); in decaying wood and under the bark (*Dicranomyia rara, D. macateei, D. dumetorum*, Discobola, *Limnobia cinctipes, L. annulus, Rhipidia bryanti, R. fidelis*, and others); in fungi (*Limnobia xanthoptera, L. triocellata*, and sometimes *L. cinctipes*). The Hawaiian species *Dicranomyia foliocuniculator* Swezey mines in the leaves of gesneriaceous plants (Cyrtandra), forming long, tortuous tunnels.

Antochini: Aquatic, very similar to habitat of *Dicranomyia simulans* as described above, in silken cases on rocks that are thoroly wet (Elliptera); in submerged stems of *Rumex aquaticus* (*Rhamphidia longirostris*); in slow or rapid water on stones (Antocha); in moist earth or mud (*Toxorhina muliebris*); under the bark of decaying trees (*Elephantomyia westwoodi, Teucholabis complexa*).

Eriopterini: In moist earth or mud in close proximity to water (most species of the tribe — *Ormosia nubila, O. innocens, O. meigenii, O. nigripila, Erioptera chlorophylla, E. vespertina, E. septemtrionis, Molophilus pubipennis, Helobia hybrida, Gonomyia sulphurella*, and others); in earth of a somewhat drier nature (Chionea); in wet sandy soil (*Gonomyia alexanderi*); under the bark of decaying trees (*Gnophomyia tristissima*). The tropical species of Trentepohlia live in decaying vegetable matter, or, as in the case of the two American species *T. bromeliadicola* and *T. leucoxena*, in the water gathered in the axils of bromeliaceous plants.

Limnophilini: Aquatic (*Limnophila luteipennis* and others); in wet or saturated organic mud in close proximity to running or standing water (most species of the tribe — *Limnophila macrocera, L. tenuicornis, L. tenuipes, L. recondita, L. adusta*, Adelphomyia, and others); in decaying wood and under the bark (*Epiphragma fascipennis, E. solatrix, E. picta, Limnophila unica*, and others); in fungi (*Ula elegans, U. macroptera*, and others).

Hexatomini: Aquatic in the early larval stages, going to land only when fully grown and ready to transform to the pupal condition; in sandy soil in close proximity to rather large streams or rivers (*Eriocera spinosa, E. longicornis, E. fultonensis, E. tristis, Hexatoma megacera*, and others); in organic earth and rich humus (*Penthoptera albitarsis*). As stated elsewhere, the larvae of this tribe are carnivorous, the larger species feeding on organisms as large as the nymphs of dragon-flies.

Pediciini: Aquatic or amphibious (probably all the species of the tribe — *Pedicia albivitta, P. rivosa*, Tricyphona, *Rhaphidolabis tenuipes, R. flaveola, Dicranota bimaculata*, and others). As stated elsewhere, the larvae of this tribe are carnivorous, those of the species of Dicranota feeding on worms of the genus Tubifex.

Cylindrotominae: Aquatic, on submerged plants and similar places (*Phalacrocera replicata*); in mountain torrents on the aquatic moss Fontinalis (*Triogma trisulcata*). Terrestrial, on leaves of flowering plants, as species of Anemone, Stellaria, Viola, and other genera (*Cylindrotoma distinctissima*); on mosses of the genus Hypnum and related species (*Liogma*

[9] The following entomologists have kindly supplied the writer with specimens or data on certain species as follows: Johannsen, *Limnobia fallax*; Greene, *L. indigena*; Shannon and Knab, *Rhipidia bryanti*; Mrs. Tothill, Toxorhina; Johnson and Shannon, Elephantomyia; Hyslop, Oropeza and Longurio.

glabrata, L. nodicornis). The larvae of this group are usually bright green in color, are variously armed with spines and filaments, and bear a striking resemblance to the caterpillars of certain Lepidoptera.

Dolichopezini: In decaying wood (*Brachypremna dispellens*); underneath the moss *Hedwigia albicans*, but also in moist earth (Oropeza).

Ctenophorini: In decaying wood (*Ctenophora apicata* and others); in wood that is but slightly decayed (Tanyptera). The species of the latter genus bore into the wood of Acer and other hardwood trees while it is still in a good state of preservation, and represent the maximum development of the wood-boring habit in this family so far as is known to the writer.

Tipulini: Aquatic, but going to the land for pupation (*Tipula abdominalis, T. cayuga, T. tephrocephala*, and others); semi-aquatic or amphibious (*Holorusia rubiginosa*, Longurio, *Tipula bella, T. sayi, T. strepens, T. tricolor*, and others); under moss growing on moist earth (*Tipula nobilis, T. collaris*, and others); in drier soil feeding on the tissue of plants (*Tipula ultima, T. bicornis, T. cunctans, Nephrotoma ferruginea*, and others); under bark of prostrate trees in an advanced state of decay (*Tipula usitata, T. trivittata*, and others). The green larvae of an undetermined Tipula (possibily *T. iroquois*) live in submerged mosses (Hypnum, sens. lat.) in rapid-flowing streams where the current is very strong; here they are associated with a society which is characteristic of such places — may-flies (*Iron fragilis*), black-flies (Simulium), net-winged midges (Blepharocera), Stratiomyiidae, Anthomyiidae, *Limnophora torreyae*, and a host of other forms.

The larva of the crane-fly has a segmented body, with about twelve apparent segments; the head is a composite of several small sclerites. The larva is wormlike in appearance and is legless, and the head is capable of retraction within the body except in the Ptychopteridae and the Rhyphidae. At the caudal end of the body is the disk bearing the two spiracles, or stigmata. Except in the Limnobiini this disk is surrounded by a varying number of fleshy lobes — two in the Pediciini (fig. 122, E), four in many of the Tipulinae, the Cylindrotominae (fig. 122, G), the Antochini, and the Hexatomini (fig. 122, F), five in the Eriopterini, the Limnophilini (fig. 122, D), and many of the Tipulinae, and six or eight in other species. Beneath the spiracular disk are the gills, usually four or six in number. These are long and filiform in the aquatic species (fig. 122, I), and correspondingly reduced or entirely absent in the less aquatic and the terrestrial species. In the Ptychopteridae (fig. 122, A) the spiracles are borne at the tip of a long, extensile tube, which is raised above the surface film while the larva feeds at will beneath the water; the gills, two in number, are about midlength of the tube. The larva of Trichocera has a pair of thoracic stigmata in addition to the caudal spiracles.

In many crane-fly larvae the body is provided with fleshy transverse folds, which are armed with chitinized points and roughened areas to assist in locomotion. These are best developed in the Pediciini (fig. 122, E), in which they resemble pseudopodia. The larvae of the Cylindrotominae (fig. 122, H) are covered with spines and thorns of various shapes.

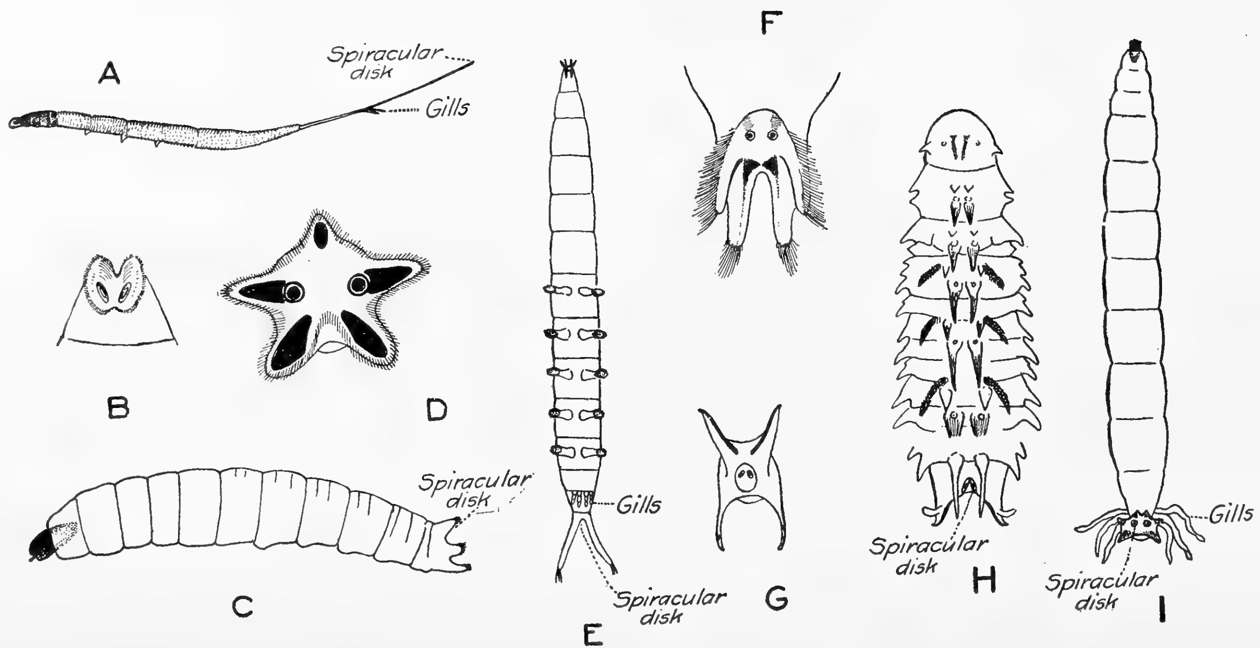


FIG. 122. LARVAE OF VARIOUS SPECIES OF CRANE-FLIES

A, *Bittacomorpha clavipes* (Ptychopteridae), lateral aspect; after Hart. B, *Dicranomyia simulans* (Limnobiini), spiracular disk; after Needham. C and D, *Ula elegans* (Limnophilini), lateral aspect and spiracular disk. E, *Dicranota bimaculata* (Pediciini), ventral aspect; after Miall. F, *Hexatoma megacera* (Hexatomini), spiracular disk. G and H, *Liogma nodicornis* (Cylindrotominae), spiracular disk and dorsal aspect. I, *Tipula* sp., *tricolor* group (Tipulini), dorsal aspect

THE PUPA

The pupal stage is of short duration, usually a week or two, and is spent in or near the larval habitat. In the case of aquatic species the pupal existence is passed in the earth adjoining the water in which the larva lived, except perhaps in the case of Antocha, which may pupate directly in the water. The larvae of many species of Limnobiini, of Antochini, and in a slightly lesser degree of most other groups, spin a silken case, or cocoon, in which to spend the pupal period. The pupae are more or less active and often wriggle about with great agility.

On the thoracic dorsum the pupa bears the two breathing horns (fig. 123), which are variously formed in the different groups. They are short, blunt, and flattened in the Limnobiini (fig. 123, B), moderately elongate and cylindrical in the Eriopterini, the Limnophilini (fig. 123, C and D), and the Tipulini (fig. 123, H), short and truncated at their apices in the Pediciini (fig. 123, E). In the Ptychopteridae (fig. 123, A), one of the two horns is atrophied, while the other is enormously elongated and serves the same function as the extensile breathing tube of the larva. In addition to the thoracic spiracles, the pupae of the Hexatomini (fig. 123, F), the Eriopterini, and some others have conspicuous lateral abdominal stigmata.

The abdominal segments generally have rows of spines or chitinized points arranged transversely around the caudal margin (fig. 123, H), which help the insect in moving about and serve to keep the tender part of the abdomen from contact with the earth. In the Hexatomini (fig. 123, F) similar spines are developed on the thorax, on the head, and even on the face of the compound eye. In the Cylindrotominae (fig. 123, G) these spines are very highly developed. Smooth-bodied pupae, such as are found in the Limnobiini, are usually inclosed in a silken tube which keeps them from contact with the soil.

When the insect is ready to transform to the final, or adult, stage, the pupa makes its way to the surface of the earth, to which it remains attached by the caudal part of the abdomen. The thoracic notum then splits down the mid-dorsal region in a straight line, and thru this opening the adult fly emerges. Before the chitin of the body hardens, the insect is very weak and pallid, but in a short time the body expands to its full size and becomes hardened and fully colored, and the dangerous period of transformation is over.

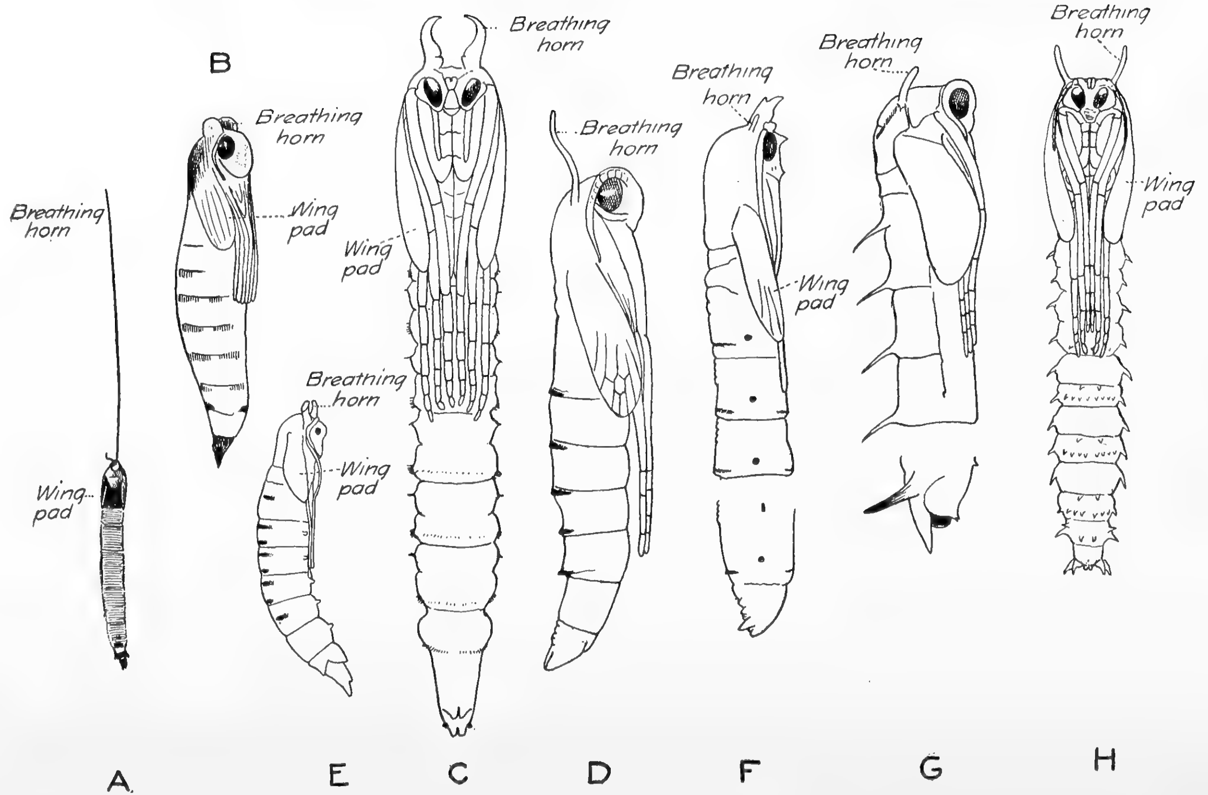


FIG. 123. PUPAE OF VARIOUS SPECIES OF CRANE-FLIES

A, *Bittacomorpha clavipes* (Ptychopteridae), dorsal aspect; after Hart. B, *Limnobia cinctipes* (Limnobiini), lateral aspect. C, *Epiphragma fascipennis* (Limnophilini), ventral aspect; after Needham. D, *Ula elegans* (Limnophilini), lateral aspect. E, *Dicranota bimaculata* (Pediciini), lateral aspect; after Miall. F, *Hexatoma megacera* (Hexatomini), lateral aspect. G, *Liogma nodicornis* (Cylindrotominae), lateral aspect. H, *Tipula ultima* (Tipulini), ventral aspect; after Needham

REARING THE IMMATURE STAGES

As has been stated elsewhere, the author believes the most important work yet to be done in entomology is the study of the immature stages of the various groups of insects. In most cases it is necessary to rear the immature stages thru to the adult in order to be certain of the species, and this process of bringing the larva to the perfect condition is often attended with many difficulties. The author has spent several years in rearing the local Tipulidae, and a general statement of the methods adopted is here given.

It should be borne in mind that the bringing of the larvae from their natural habitat into the warmth of the laboratory accelerates their development, and the adults emerge in the breeding cages a week or two earlier than in nature.

Aquatic forms

The aquatic forms are among the most difficult to rear, especially the species living in rapid, well-aërated water. It must be understood at the start that practically all crane-flies require earth, sand, or a similar solid material in which to pupate, and it is often very difficult to provide rushing torrents for the larval life together with solid earth for the pupal existence. Breeding cages, consisting of wire cylinders the ends of which are covered with cheesecloth, have been used with considerable success. The mesh must be of sufficient fineness to retain the larvae inside, but not so small as to exclude the food that is carried in the current; however, since this food is microscopic or very small, a fine mesh is sufficient to allow its entry into the cage. The whole cage can be transferred to the natural haunt of the larva and kept under observation until the adult insect emerges. The main difficulties with this method are the danger of smothering the insect by deposition of silt during high water, the washing away of the entire outfit during storms, and the inconvenience, in most cases, of having to make many long trips to the scene of rearing before the final result is obtained. In almost all cases when the species could be reared by the use of such breeding cages, the writer has been able to get adult flies by placing the full-grown larvae in medium-sized (four-ounce) shell vials together with some earth from their natural habitat. In order to prevent evaporation, small caps of cheesecloth may be fas-

tened over the ends of the vials by means of rubber bands, sufficient water being added every day or two to restore the balance lost by evaporation. If the specimens are fully grown or nearly so, they soon pupate and finally emerge.

Species that live in extremely rapid waters (as the tipuline larva described on page 839) are almost impossible to rear. The best results have been obtained by placing the fully grown larvae in the folds of a saturated piece of cheesecloth in a jar, the jar being corked to prevent any evaporation — which is here, as elsewhere, the most frequent source of danger and death to the larvae. Several specimens of crane-fly larvae may be placed in a single vial except in the case of the carnivorous forms (Hexatomini, Pediciini), in which case care should be taken to isolate single specimens lest they kill one another and the decaying of their bodies destroy the remaining life in the vials.

Mud-inhabiting forms

The majority of crane-fly larvae are mud-inhabiting forms. Most of these belong to the small and inconspicuous Limnobiinae, and are rarely seen by the collector. To procure them it is necessary to sift the mud of their haunts and examine the contents of the sieve with great care. A small-mesh wire sieve is about the most satisfactory form to use, and the mud can be washed in small quantities and the remaining contents of the sieve easily scrutinized. As they are found, the larvae can be placed in water in small watch crystals and finally removed to individual breeding jars. The methods of breeding described above are applicable to these, and if the larvae are large and nearly grown it is not difficult to rear them.

Fungus-inhabiting forms

The forms inhabiting fungi (species of Limnobia and Ula, and some others) are easily reared by placing the whole fungus in a large pint or quart jar about one-fourth filled with pure sand. This sand takes up the juices as the fungus decays, and at the same time furnishes a good place for pupation of the species. The jars should be kept air-tight to retain a balance in moisture conditions.

Wood- and bark-inhabiting forms

The forms inhabiting wood and bark (Ctenophora, Tanyptera, and others) may be reared by placing pieces of their natural habitations in a large closed jar and leaving them undisturbed. Pupation takes place in the burrows of the larvae.

THE ADULT FLIES

STRUCTURE

The head

The head is the first, or anterior, region of the body. It bears the mouth parts, the antennae, the compound eyes, and, when they are present, the simple eyes, or ocelli.

The sclerites

The sclerites, or segments, composing the head are approximately the same as in other insects, consisting of a prominent dorsal sclerite which surrounds the compound eyes, the *epicranium.* This is further divided into regions which may be located generally as follows: The *fronto-clypeus* is located on the dorso-cephalic aspect of the head, between the labrum and the region of the vertex. It consists of the united front and clypeus, the suture between them having disappeared. The *labrum,* or upper lip, is often present as a chitinized linear structure lying anterior to the fronto-clypeus and attached to the ventral margin of the clypeal region of the latter. The *vertex* occupies the dorsal region between the compound eyes, and, when they are present, includes the ocelli, or simple eyes. On or near its anterior part it bears the antennae (page 848), inserted in depressions, the *antennal fossae.* In many species with elongate antennae, especially in Eriocera, Macromastix, and some other genera, the vertex bears a distinct tubercle, the *vertical tubercle,* which is often deeply bifid. In *Geranomyia cornigera* Alex. (Philippine Islands) the vertex bears a curious elongate fleshy lobe. Very rarely this sclerite bears three simple eyes, or ocelli, which are discussed elsewhere (page 854). The *genae,* or cheeks, occupy the sides, or lateral parts, of the head, ventrad and mesad of the compound eyes. The ventro-caudal region of the head is made up of the *postgenae.* The dorso-caudal region is the *occiput.*

The mouth parts

In many species in widely separated tribes, the anterior, or frontal, part of the head is produced into a short, cylindrical rostrum, which is in most cases nearly if not quite as long as the head itself. Such a frontal prolongation occurs in Rhamphidia (fig. 124, B and C), in some tropical species of Teucholabis (Antochini), in Opifex (Eriopterini) and Ornithodes (Pediciini), and in most Tipulini (fig. 124, E). In these

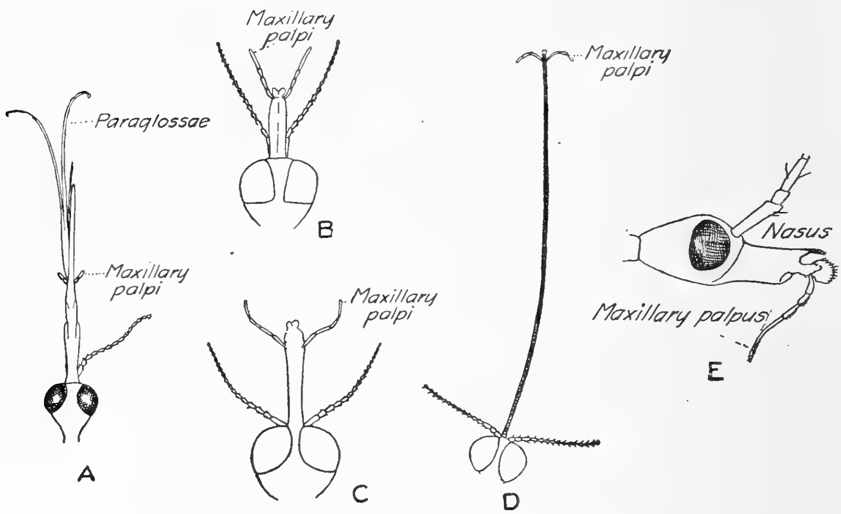


FIG. 124. MOUTH PARTS OF VARIOUS SPECIES OF CRANE-FLIES

A, *Geranomyia canadensis*, male, ventral aspect. B, *Rhamphidia flavipes*, male, ventral aspect. C, *Rhamphidia mainensis*, male, ventral aspect. D, *Elephantomyia westwoodi*, male, ventral aspect. E, *Tipula apicalis*, male, lateral aspect

cases the mouth parts are borne at or near the tip of the prolongation. In the Tipulini there often appears near the end of the prolongation, on the dorsal side, a small tubercle bearing a brush of long hairs (fig. 124, E). This is the *nasus*, or "nose." The most generalized condition of the mouth parts in this group of flies is seen in certain members of the primitive group Tanyderidae, in which the labrum, the maxillae, the labium, and possibly the mandibles, are distinct and styliform (Alexander, 1913 a:332–333).

The mouth parts and the head capsule of the Diptera have been studied recently by Peterson (1916). The following summary of the mouth parts is taken largely from his paper:

The *maxillae* are the paired organs lying below the labrum and above the labium, one on either side. In generalized forms, such as Trichocera, they consist of a small triangular *cardo*, an elongate *stipes* bearing the needle-like *galea*, and the *palpus*. The maxillary palpi are primitively five-segmented but in almost all crane-flies only four segments are apparent; in certain cases the reduction in segments is rather extreme; this is discussed more in detail below. In the Limnobiini (Limnobia, Geranomyia) the stipites are entad of the postgenae and have their proximal ends united. In the Tipulini (Tipula) the two stipites are completely united along their inner margin to form a single median plate. The galeae are prominent in Trichocera, but are very reduced in Geranomyia and are entirely lacking in Tipula.

The *labium*, or lower lip, is the ventral, or posterior, unpaired organ. It consists of a basal immovable part, made up of the *mentum* and the *submentum*, and a movable part, or *ligula*, the basal sclerites of which are called by Peterson the *thecae*, the *furcae*, and so on, and the distal parts the *glossae* and the *paraglossae*.

The *epipharynx* lies behind the labrum and fuses with it to form the *labrum-epipharynx*. The *hypopharynx* is the prolonged cuticular lining of the opposite side of the mouth cavity. In such genera as Trichocera, Limnobia, and Tipula, studied by Peterson, the labrum-epipharynx and the hypopharynx are short, but in Geranomyia, which has an elongate rostrum, these parts are correspondingly elongated.

There are two tribes containing one or more genera in which the mouth parts are greatly elongated, being in many instances longer than the remainder of the body. In the tribe Limnobiini the genus Geranomyia is thus characterized, and in the tribe Antochini the genera Elephantomyia, Rhampholimnobia, Ceratocheilus, and Toxorhina. These may be discussed briefly.

In Geranomyia (fig. 124, A) the most evident parts of the beak are styliform and greatly elongated, consisting of the labrum-epipharynx, the hypopharynx, and the conspicuous divergent lips, the paraglossae, which extend far beyond the other elements; the maxillary palpi are located far back on the organ at about one-third its length, and are reduced in

number of segments from four in the generalized subgenus Tetraphana to one in the subgenus Monophana. In Elephantomyia (fig. 124, D), Rhampholimnobia, Ceratocheilus, and Toxorhina, the rostrum consists of a much elongated tube which bears the reduced mouth parts and the maxillary palpi at the extreme apex; in Elephantomyia the maxillary palpi are three-segmented, while in Toxorhina they are apparently single-segmented.

Those species of Geranomyia, Elephantomyia, and Toxorhina whose feeding habits are known, all feed on the nectar of tubular flowers, such as the Compositae, the Apocynaceae, the Ericaceae, the Umbelliferae, the Rhamnaceae, and the Lauraceae.

The maxillary palpi are generally four-segmented; in the primitive group Tanyderidae they are five-segmented. By reduction there are found one, two (fig. 124, A), three, or four segments, respectively, in the four subgenera of Geranomyia; there are three in Elephantomyia (fig. 124, D), and apparently only one in Toxorhina. The segments in most Limnobiinae are approximately subequal in size, but in the genus Pedicia and in the subfamily Tipulinae (fig. 124, E) the fourth segment is greatly elongated, whiplash-like, and usually longer than the three preceding segments taken together. The labial palpi are two-segmented and conspicuous in species of Trentepohlia.

The antennae

The antennae of crane-flies present many interesting conditions, both in the number of the segments of which they are composed and in their structure, and many generic names have been based on these conditions — Trichocera, Rhipidia, Trimicra, Rhabdomastix, Sigmatomera, Ctedonia, Polymera, Hexatoma, Eriocera, Cylindrotoma, Phalacrocera, Megistocera, Ctenophora, and others.

The antennae are inserted on the vertex between the compound eyes. The diversity in their structure is considerable, and consists of great elongation of the organ, constriction of the segments, and the appearance of pectinations and flabellate formations. These are sexual characters only and are confined to the male sex. Elongation of the antennae occurs in many widely-separated tribes; moderate elongation is found in a wide range of native Ptychopteridae, in Trichocera, and in the tipuline genera Atarba, Ormosia, Molophilus, Limnophila, Penthoptera, Dicranota,

Nephrotoma, and Tipula; great elongation, in which the organ may be two or more times as long as the whole body, is found in a few native species of Eriocera (fig. 125, F), and in some exotic genera, as Rhabdomastix, *sens. str.*, the Old World species of Megistocera, and a few species of Macromastix. The flagellar segments are constricted at their middle in the genus Polymera, producing the multi-segmented appearance which gives the genus its name; in Sigmatomera some of the flagellar segments are reniform or shaped like a recumbent S. In many species of Ormosia (*O. monticola*, *O. divergens*, *O. megacera*, *O. mesocera*) the elongated antennae are subnodulose and strongly suggest the beadlike condition obtaining in the Cecidomyiidae. In Trimicra the three terminal segments are abruptly smaller than the remainder of the flagellum; in some species of Stygeropis it is the terminal segment only that is so reduced. Pectinations and flabellate formations are found in the antennae in many genera — Rhipidia (fig. 125, A and B), Gynoplistia, Cerozodia, Ctedonia, most of the genera of the tribe Ctenophorini (fig. 125, L and M), and several genera of the tribe Tipulini, such as Ptilogyna and Ozodicera.

The two basal segments of the antennae are quite different in shape from those that follow, and are called the *scapus*, or *scape*. The scape is often considerably enlarged, especially in those species with elongate antennae — in the genera Rhabdomastix, Eriocera (fig. 125, F), Megistocera, and others. The second segment of the scape is usually shorter than the first, and in the species with elongate antennae it is usually short and cup-shaped (fig. 125, F, G, and H), a condition known as cyathiform. The whiplike part beyond the scape is the *flagellum*. The flagellum is almost always clothed with a pubescence of varying character, from straight to uncinate, from appressed to outspreading and divergent, from short to long, and often longer in the male sex than in the female. In addition to these delicate hairs there are usually strong, bristle-like hairs arranged in a more or less complete whorl, or verticil (fig. 125, J and O). The Tipulinae (fig. 125, L–O) have a more or less complete whorl of these strong hairs, which are absent in Stygeropis (fig. 125, N) and in Holorusia and form good generic characters in a difficult group of the family. In many species of Gonomyia (*G. sulphurella* [fig. 125, E], *G. manca*, *G. pleuralis*, *G. amazona*, and others), and in some species of Erioptera (subgenus Empeda), the verticillate hairs on the male antennae are exceedingly elongated and conspicuous.

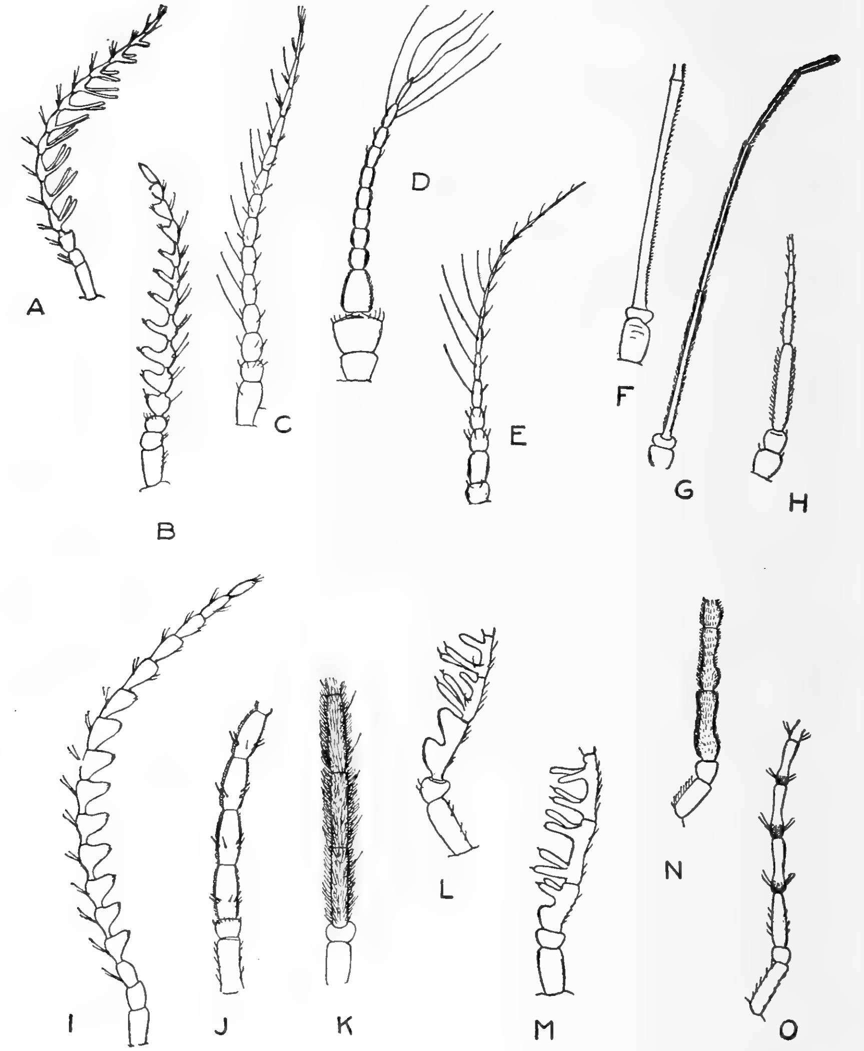


FIG. 125. ANTENNAE OF VARIOUS SPECIES OF CRANE-FLIES

Limnobiinae: A, *Rhipidia maculata*, male; B, *Rhipidia fidelis*, male; C, *Limnobia tristigma*, male; D, *Toxorhina brasiliensis*, male; E, *Gonomyia sulphurella*, male; F, *Eriocera spinosa*, male, three basal segments; G, *Hexatoma megacera*, male; H, *Hexatoma megacera*, female

Cylindrotominae: I, *Liogma nodicornis*, male; J, *Phalacrocera tipulina*, male, six basal segments; K, *Cylindrotoma tarsalis*, male, five basal segments

Tipulinae: L, *Tanyptera frontalis*, male, five basal segments; M, *Ctenophora angustipennis*, male, five basal segments; N, *Stygeropis fuscipennis*, male, four basal segments; O, *Tipula mainensis*, male, six basal segments

The following additional notes on chiefly local species are presented:

Tanyderidae: In *Protoplasa fitchii*, of the family Tanyderidae, the antennae are 16-segmented; the scape is enlarged, and the flagellar segments are elongate-oval with a dense pubescence and verticillate bristles. In other Tanyderidae the number of segments ranges from 15 to 25.

Ptychopteridae.— In the genus Bittacomorpha of the family Ptychopteridae, the antennae are apparently 20-segmented. In the males they are elongated; the scape segments are short, the second one being short-cyathiform; the flagellar segments are greatly elongated, with a long outstretched pubescence and no bristles. In Ptychoptera the antennae are 16-segmented, with distinct scattered bristles and a short, somewhat uncinate, pubescence.

Rhyphidae.— In the genus Trichocera of the family Rhyphidae, the antennae are almost hairlike, tho finely pubescent.

Tipulidae, Limnobiinae.— Limnobiini: In the tribe Limnobiini the antennae are 14-segmented. In Limnobia (fig. 125, c) the segments have numerous bristles and a close, dense pubescence; the terminal segment is usually much attenuated, about as long as the two preceding segments taken together, often presenting a biarticulate appearance. In Rhipidia a curious modification of the organ is found, the flagellar segments being bipectinate in the subgenus Rhipidia (fig. 125, A), unipectinate in the subgenus Monorhipidia (fig. 125, B), and from subpectinate to almost normal in the subgenus Arhipidia.

Antochini: As a rule the antennae are 16-segmented in the tribe Antochini. The first scape segment is rather elongated, the second is oval, not markedly cyathiform. The flagellar segments are rounded-oval or elongate (in the males of most species of Atarba), with bristles and a short, dense pubescence. The antennae are of this normal structure in the genera Rhamphidia, Antocha, Dicranoptycha, Atarba, and Teucholabis. In Elephantomyia there are 15 segments; the first segment of the scape is only a little larger than the second; the first flagellar segment is apparently formed by the fusion of two segments, and bears three strong hairs on the lower face in a line; the remaining segments of the flagellum are elongate-cylindrical, with strong verticils. In the genera Toxorhina (fig. 125, D) and Ceratocheilus there are but 12 segments; the second scape segment is larger than the first; the first flagellar segment is obconical, and is apparently formed by the fusion of five segments,

altho the segment is very short and is destitute of verticils; the seven succeeding flagellar segments are short-cylindrical, without verticils; the terminal two segments are more elongated and each bears about three very long hairs.

Eriopterini: Normally there are 16 antennal segments in the tribe Eriopterini. In some genera both elongate and short antennae are found in the same group, as in Ormosia, *sens. str.* In Chionea, Cladura, Pterochionea, and Crypteria the number of antennal segments is reduced, due to the fusion of several segments to make up the basal segment of the flagellum — as in the case of Toxorhina, already discussed — this fusion segment including usually five segments.

Limnophilini: In the tribe Limnophilini the antennae are normally 16-segmented; in the genus Ula they are 17-segmented. In Limnophila and Epiphragma are found some species with elongate and others with short antennae. In *Limnophila macrocera* and some other species, the segments of the flagellum are provided with abundant outstretched hairs. In *Adelphomyia cayuga* the basal segments of the flagellum are fused into an indistinct fusion-segment; the other local species of this genus have normal antennae.

Hexatomini: In *Hexatoma megacera* (fig. 125, G) the antennae of the male are 6-segmented, the flagellar segments being elongate; in the female (fig. 125, H) the antennae are apparently 8-segmented. In Eriocera there are many species with short antennae (*Eriocera brachycera, E. fuliginosa, E. fultonensis*, and others), species with the antennae intermediate in length (such as *E. eriophora*), and numerous species with greatly elongated antennae (*E. spinosa, E. californica, E. longicornis*, and others). In *E. spinosa* (fig. 125, F), *E. longicornis*, and others, the lower surface of the basal flagellar segment is provided with numerous spines, regularly spaced, pointing toward the tip of the organ; the manner in which these spines are used in extricating the organ from the antennal sheath of the pupa is described by Alexander and Lloyd (1914). In *E. wilsonii* the antennae are likewise elongated in the male sex, but are provided with a strong pubescence, the spines being quite lacking. Most species of Eriocera have short antennae in both sexes.

Pediciini: In the genera Pedicia and Tricyphona of the tribe Pediciini, the antennae are 16-segmented; in the genus Dicranota and the subgenera

Plectromyia and Rhaphidolabis, they are 13-segmented; and in the subgenus Rhaphidolabina they are 15-segmented.

Tipulidae, Cylindrotominae.— The antennae are apparently 16-segmented in the genus Cylindrotoma of the subfamily Cylindrotominae, and 17-segmented in the genera Phalacrocera and Liogma. In *Cylindrotoma tarsalis* (fig. 125, K) the flagellar segments in the male are elongate-cylindrical, with a dense erect pubescence and a very few scattered bristles. In *Phalacrocera tipulina* (fig. 125, J) the condition is fairly similar, but there is a distinct verticil of stiff bristles near the bases of the segments, a condition strongly suggesting that found in the genus Tipula. In *Liogma nodicornis* (fig. 125, I) the intermediate flagellar segments are rather strongly pectinate, with a dense, pale pubescence and several long bristles on the back face of each segment, and with shorter, weaker bristles at the apex of the pectination.

Tipulidae, Tipulinae.— Dolichopezini: The antennae in Dolichopeza, Oropeza, Brachypremna, and other genera of the tribe Dolichopezini, are normally 13-segmented; in the American species of the genus Megistocera the antennae are 8-segmented. The organ is often considerably elongated, exceedingly so in Old World species of Megistocera. In Brachypremna the antennae are correspondingly short and tiny.

Ctenophorini: In the tribe Ctenophorini the antennae are 13-segmented. In the male sex they are curiously pectinated or fanlike, tho differing in construction from those in Rhipidia already discussed (page 851). In *Ctenophora angustipennis* (fig. 125, M) the first segment of the flagellum bears a basal pectination and two apical pectinations, each tipped with a bristle; the second and succeeding segments have a basal pair of pectinations, each tipped with a bristle, and a pair of apical appendages, untipped. In *Tanyptera frontalis* (fig. 125, L) the first segment of the flagellum bears a basal and an apical pectination; the second and succeeding segments have a basal pair of pectinations, each tipped with a bristle, and the single shorter apical pectination is not thus protected.

Tipulini: Normally the antennae in the tribe Tipulini are 13-segmented; in some species of Nephrotoma there are 16 or 19 segments in the male. In most species of this tribe each flagellar segment has a strong basal swelling armed with a verticil of strong bristles; this knobbed condition reaches its maximum development in the species of the *monilifera* group (of tropical America), in which a beadlike form is produced. Other

species of Tipula and some species of Nephrotoma have the segments deeply incised on the under face, producing a serrated appearance. In Stygeropis (fig. 125, N) and Holorusia, and to a lesser extent in Longurio, the verticils are lacking. *Tipula mainensis* (fig. 125, O) is a typical Tipula and illustrates this verticillate condition.

The eyes

On either side of the head, in all crane-flies, are the large compound eyes, made up of numerous facets, or *ommatidia*. In generalized forms the facets are large and coarse, so that the eye presents a coarsely granulated appearance; in other species the ommatidia are so small and abundant that the surface of the eye appears very smooth and regular. In most species of Tipulidae the eyes are separated by a narrow strip of the front (*dichoptic*), but in the males of some they are contiguous (*holoptic*) or nearly so, as in certain species of Rhipidia and allied groups. In some species of Erioptera (*Erioptera macrophthalma*, *E. vespertina*, *E. nyctops*, and others) the eyes of the males are much larger than those of the females and are contiguous beneath.

In most genera the eyes are large and extend backward onto the caudal part of the head. In Trichocera and Ischnothrix the vertex bears three simple eyes, or *ocelli*.

The thorax

The thorax is the second region of the body and lies between the head and the abdomen. This part of the body bears the legs, and, when they are present, the wings also. It is divisible into three subregions, as follows: the prothorax, or first segment, which bears the fore legs; the mesothorax, or second segment, which bears the middle legs and the wings; and the metathorax, or third segment, which bears the hind legs and the halteres. The upper, or dorsal, sclerites of these subregions are called the *tergites*, the *notum*, or the *dorsum*; the lateral sclerites, those on the sides of the body, are the *pleura*, or *pleurites*; those on the lower, or ventral, parts of the body are the *sternites*, or *sternum*. Each subregion has its own terminology, the prothorax having its pronotum, propleurites, and prosternum, the mesothorax its mesonotum, mesopleurites, and mesosternum, and so on. The legs borne by these respective segments likewise have the corresponding prefix applied to their parts — as the precoxa (or fore coxa), the mesocoxa (or middle coxa), the pre-

femora, the mesotibia, and so on. In addition to the thoracic segments there are some tiny sclerites between the head and the prothorax, called the *cervical sclerites* and comprising the *neck*, or *microthorax*.

The prothorax.— In the Tipulidae the pronotum, or dorsal sclerite of the prothorax, consists of two regions which are usually interpreted as being homologous to the scutum and the scutellum of the mesonotum, described and illustrated below. In this paper these regions are called the *pronotal scutum* and the *pronotal scutellum*. The propleurites are made up of the usual pleural plates, which are discussed in the description of the mesothorax; these are termed the *proepisternum* and the *proepimeron*. The sternal region of the prothorax is the *prosternum*. In the family Tipulidae the sclerites of the pronotum are usually small and insignificant, being encroached upon by the sclerites of the mesothorax. In some exotic genera, such as the tropicopolitan genus Styringomyia, the prothorax is large and of a generalized structure. In entomological literature the pronotum is usually spoken of as the "neck" or the "collare."

The mesothorax.— The mesothorax is the principal region of the thorax in the Tipulidae. The mesonotum, or upper part, is divided into two sclerites, which are again divided so as to appear as four — the prescutum, the scutum, the scutellum, and the postnotum.

The *prescutum* is the anterior, or first, subdivision. In crane-flies it is the largest single region of the thorax, lying behind the pronotum and before the transverse, or V-shaped, suture. It may be very flat and depressed, as in the South African genus Platylimnobia, or very high and gibbous, as in *Dicranomyia globithorax*, *D. gibbera*, and other species; or it may jut far cephalad over the pronotum, as in Conosia and in many species of Trentepohlia. In the subgenus Conorhipidia of the genus Rhipidia, which includes two species from tropical America, the prescutum is elevated into a high conical point, which is very remarkable but is suggested in other species of the same genus, as, for instance, *Rhipidia domestica*. The prescutum is usually striped in various ways, a common pattern being three stripes, one in the middle and two shorter ones on the sides. The spaces between these stripes often bear setigerous punctures, with setae of various forms and sizes. In many genera the prescutum bears two shiny dots, called *tuberculate pits* (fig. 126, B). In certain groups,

as in many species of Limnophila and in the eriopterine series allied to Gonomyia (Gonomyia, Rhabdomastix, and other genera), these pits lie one on either side of the median line of the prescutum, at the extreme cephalic margin; in other groups, as in the eriopterine series allied to Erioptera (Erioptera, *sens. str.*, Empeda, and other genera), they are found on the dorsum of the prescutum, about midlength of the segment. These pits are the double, or paired, dots of Osten Sacken.

The *pseudosutural foveae* (fig. 126, B) are prominent depressions on the sides of the prescutum, in front, lying just above the anterior spiracles,

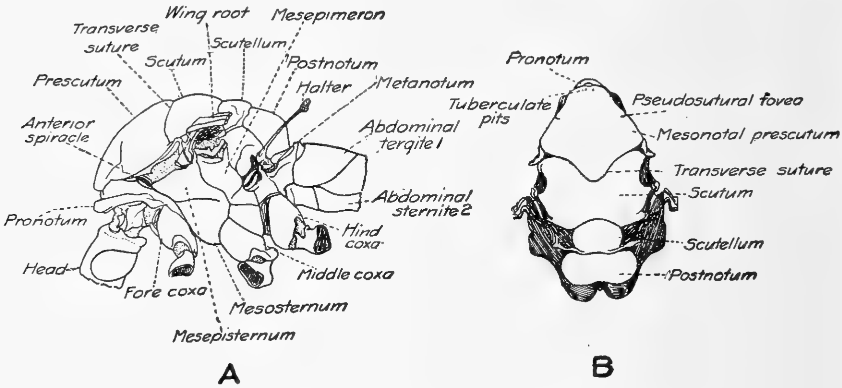


FIG. 126. THORAX OF TIPULA

A, Lateral aspect; B, dorsal aspect. Adapted from Snodgrass

usually in the area before the ends of the short lateral stripes and at the sides of the longer median stripe. These structures have been called the *humeral pits*.

The *scutum* is the second subdivision of the mesonotum. It lies just behind the V-shaped suture and is usually divided into two lateral lobes by a shallow median depression.

The *scutellum* is the third subdivision of the mesonotum. It is a small transverse segment, lying just behind the lobes of the scutum and before the postnotum.

The *postnotum* is the fourth and last subdivision of the mesonotum. It is a large and prominent sclerite situated behind the scutellum, appearing

almost vertical in position. The dorsal part of the postnotum lies between the halteres, and the lateral part between the wings and the scutellum in front and the halteres and the metapleura behind. This region is often erroneously considered as being the metanotum.

The *pleuron* of the mesothorax (fig. 126, A) consists of the mesepisternum and the mesepimeron. The *mesepisternum* is the plate making up the anterior part of the pleuron. It is bounded caudad by the mesepimeron and ventrad by the mesosternum. Its dorso-cephalic angle is close to the mesothoracic spiracle. The *mesepimeron* is the plate making up the posterior part of the pleuron. It is a long sclerite, lying underneath the wing base and bordered behind by the mesonotal postnotum and the metepisternum.

The *sternum* of the mesothorax is usually prominent, lying beneath the pleura and bearing the middle legs.

The mesothorax bears the wings of the insect, as well as the middle legs. The details of the wing venation are discussed under a separate caption (page 860). The wings are always present in crane-flies, but they are very tiny and reduced in the genus Chionea, and in many genera and species they are so reduced as to be useless for flight. This atrophy of the wing may consist of a reduction in width only, the length being unaffected and the organ taking on a straplike appearance (as in *Tipula pribilofensis*); or there may be a reduction in both the length and the width, the wing in extreme cases (such as *Tipula chionoides*, Platylimnobia, and others) being a mere pad which is shorter than the halteres. As a result of the distortion of the wing shape there is a corresponding reduction and atrophy of the venation. In the northeastern United States and eastern Canada, all the crane-flies are full-winged except the nearly wingless Chionea, mentioned above.

The wing surface is usually provided with a microscopic pubescence, to which are due many of the opalescent reflections in crane-flies (as in Antocha, Dicranoptycha, and other genera). In addition to this microscopic pubescence there is also found, in many scattered groups of genera, a strong pubescence, which is apparent with a hand lens. The writer regards the retention of this coarse pubescence as being a primitive character. Its nature varies. In some genera it covers the whole surface of the wing — as in Ormosia, Ula, and Ulomorpha; in many species it is confined to certain of the apical cells of the wings — as in *Dicranomyia*

pubipennis, Erioptera (Empeda) pubescens, Gnophomyia luctuosa, species of Adelphomyia, the subgenus Lasiomastix of Limnophila, Bittacomorphella, certain Ptychoptera, and some species of Dolichopeza (Tricho-dolichopeza), Tipula (Trichotipula, Cinctotipula), and so on. In most crane-flies the wing veins likewise bear long hairs, which in some genera, such as Molophilus, are very long; in some species, however, the hairs are so short as to be scarcely noticeable.

The metathorax.— The only part of the metanotum, or dorsal sclerite of the metathorax, which is visible is the postnotum. This appears as a narrow, transverse sclerite between the mesonotal postnotum and the first segment of the abdomen. The pleural sclerites consist of the *metepisternum,* a very small sclerite between the metathoracic spiracle and the hind coxae, and the *metepimeron,* a small sclerite behind the halteres.

The metathorax bears the hind legs and the *halteres,* or *balancers.* The halteres are usually considered as being reduced hind wings, and serve an important function in flight. They lie just behind the wings and are of various shapes, in some species (as *Dicranomyia halterata* and *Gonomyia filicauda,* for example) being very long and slender and in other cases being short with prominent swollen knobs. In some groups with reduced wings (such as Platylimnobia) the halteres also are reduced and straplike. The halteres are retained even when the wings have been practically lost, as shown by the genus Chionea.

The legs

The legs of crane-flies are as a rule excessively elongated, which gives to the group all or almost all of its common names — *crane-fly* (from a comparison with the crane), *daddy longlegs* (the British name for the group), and so on. The leg is made up of nine segments, designated, respectively, from the body outward, as the *coxa,* the *trochanter,* the *femur,* the *tibia,* and the five *tarsal segments.*

The coxa.— The coxa is the enlarged basal segment of the leg, that of the fore leg being called the fore coxa, precoxa, or procoxa, and those of the middle and hind legs having the corresponding prefixes. In the groups with great powers of flight (Megistocera, Trentepohlia, and others) the coxae are very small, while in the species with reduced wings and consequent need of walking (as in the genera Platylimnobia, Chionea,

and others) they are very large and powerful. The coxae are often provided with a dense covering of long silky hairs.

The trochanter.— The second segment of the leg, called the trochanter, lies between the coxa and the femur and serves as a pivot between these two major segments. In Dicranoptycha, the distal margin is armed with a sharp blackened tooth which is directed inward.

The femur.— The femur is the third segment of the leg, corresponding to the thigh of higher animals. It is the largest and most powerful single element of the leg, being in many cases greatly elongated and

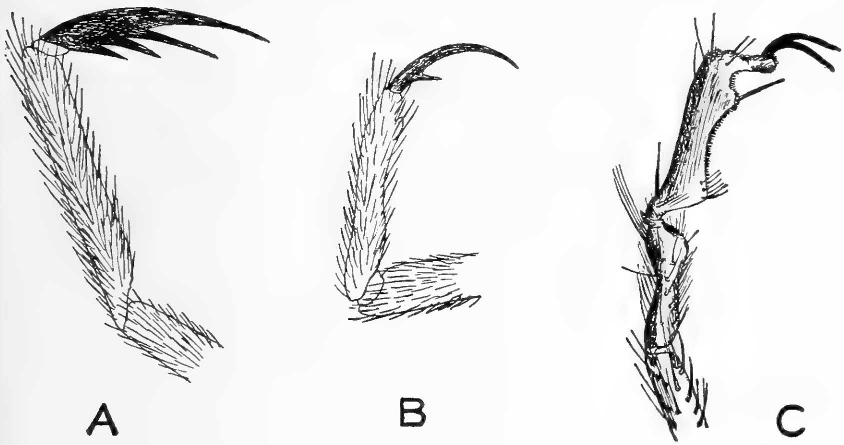


FIG. 127. FEET OF CRANE-FLIES

A, *Limnobia indigena*, male, last tarsal segment and claw. B, *Dicranomyia morioides*, male, last tarsal segment and claw. C, *Rhabdomastix flava*, male, last two segments and claw

incrassated. In some groups (as Ctenacroscelis, for example) it bears a comb of approximated spines near the distal end. In other genera, especially in Trentepohlia, the femur is often armed with groups or rows of stiff bristles or short spines, which furnish valuable specific characters.

The tibia.— The tibia is the fourth segment of the leg, situated between the femur and the first (metatarsal) segment of the tarsus. Next to the femur it is the longest single element of the leg. In many groups a pair of spines, or spurs, are borne at the tip, called the *tibial spurs*, and these

are of great importance in classification. These spurs are lacking in the tribes Limnobiini, Antochini, and Eriopterini, but are present in the remainder of the Tipulidae tho in some cases they are so small as to require a low-powered microscope for their detection.

The tarsal segments.— The tarsus, or foot of the fly, is made up of the terminal five segments. The first of these segments is the longest and is called the *metatarsus*. The remaining segments gradually decrease in length to the last, which bears the *claws*, or *ungues*, and, when it is present, the *empodium* between the claws. In Bittacomorpha the metatarsus is swollen and bladder-like. In one species of Lecteria the metatarsus bears a group of three stout spines at the extreme base. The claws of most crane-flies are quite smooth (fig. 127, C, Rhabdomastix), but those of species of the tribe Limnobiini have teeth on the ventral side (fig. 127, A, Limnobia; fig. 127, B, Dicranomyia). A similar condition is found in certain Dolichopezini, such as Brachypremna and Tanypremna, but not in Megistocera.

The transverse suture

The transverse suture is considered one of the important characters for use in distinguishing the Tipulidae from related families of flies, such as the Dixidae, the Mycetophilidae, and others. It is in the shape of a low V, and separates the mesonotal prescutum from the scutum.

The wings and their venation

The wings of crane-flies, with their remarkably constant venation and pattern, furnish the easiest and best characters for recognition of the various forms. In the great majority of cases a glance at the wing is sufficient for the determination of the species, and it is for this reason that considerable emphasis is here placed on these organs. This paper discusses only in a rather elementary way the essentials of the wing venation, but Needham (1908) has made a critical survey of the character in all the genera of the Tipulidae known at the time his work was prepared, and his paper is absolutely essential to the student of this group of insects.

The wing is made up of a series of longitudinal veins running from the base to the outer margin and bound together at various points by cross-veins and by deflections of the longitudinal veins which produce

strong fusions at these places. The more specialized forms have an unusually strong series of cross-veins and deflections running transversely or obliquely across the wing at about two-thirds its length and generally in line with the ending of the radial sector and the inner end of the cell *1st* M_2 (discal). This strong fusion is called the *cord,* and a glance at almost any wing will enable one to pick it out immediately. The genus Pedicia (Plate XLII, 175) has the elements of the cord in almost perfect alinement, but very oblique, and here the principal parts entering in are the basal deflection of Cu_1, the basal deflection of M_{1+2}, and the *r-m* cross-vein; in most crane-flies the deflection of R_{4+5} adds another strong element to the cord, while in many genera (as Antocha, Plate XXXIII, 48, and Teucholabis, Plate XXXIII, 52 and 53) the radial cross-vein is so placed as to become still another strong element. Very often the radial sector enters in as the part nearest to the main radial vein (R_1), and here the stress falls either on the sector or on R_{2+3}, or on both. As has been pointed out by Needham, in many species the closed cell of the wing (*1st* M_2) is swung directly across the path of the cord, interrupting it like a ring on a line; the medial cross-vein and the outer deflection of M_3 are quite necessary to complete this ring, and they are always present in such cases. It is only when the inner end of the closed cell gets into alinement with the other elements of the cord, so that the ring formed by the cell is no longer needed to strengthen the wing disk, that the medial cross-vein is lost by atrophy.

The longitudinal veins.— There are six or seven longitudinal veins, named, respectively, from the front margin backward, the *costa,* the *subcosta,* the *radius,* the *media,* the *cubitus,* and the *anal veins.*

The *costa* (*C*, fig. 128, A) forms the anterior margin of the wing. It is usually much thickened, but thins out before reaching the wing apex. It is strongly united with the vein beneath it, the subcosta, by the humeral cross-vein at the base of the wing. More distally other veins end in the costa, such as Sc_1, R_1, and usually other elements of the radial field.

The *subcosta* (*Sc*, fig. 128, A), a weak vein lying between the costa and the radius, is often difficult to detect due to foldings and flexings of this part of the wing. In generalized forms it is forked, the anterior branch, Sc_1, going to the costa, and the posterior branch, Sc_2 (the subcostal cross-vein of the older authors), connecting with R_1. In the subfamily Limnobiinae, Sc_1 is usually present, and Sc_2 may be close to its tip as in

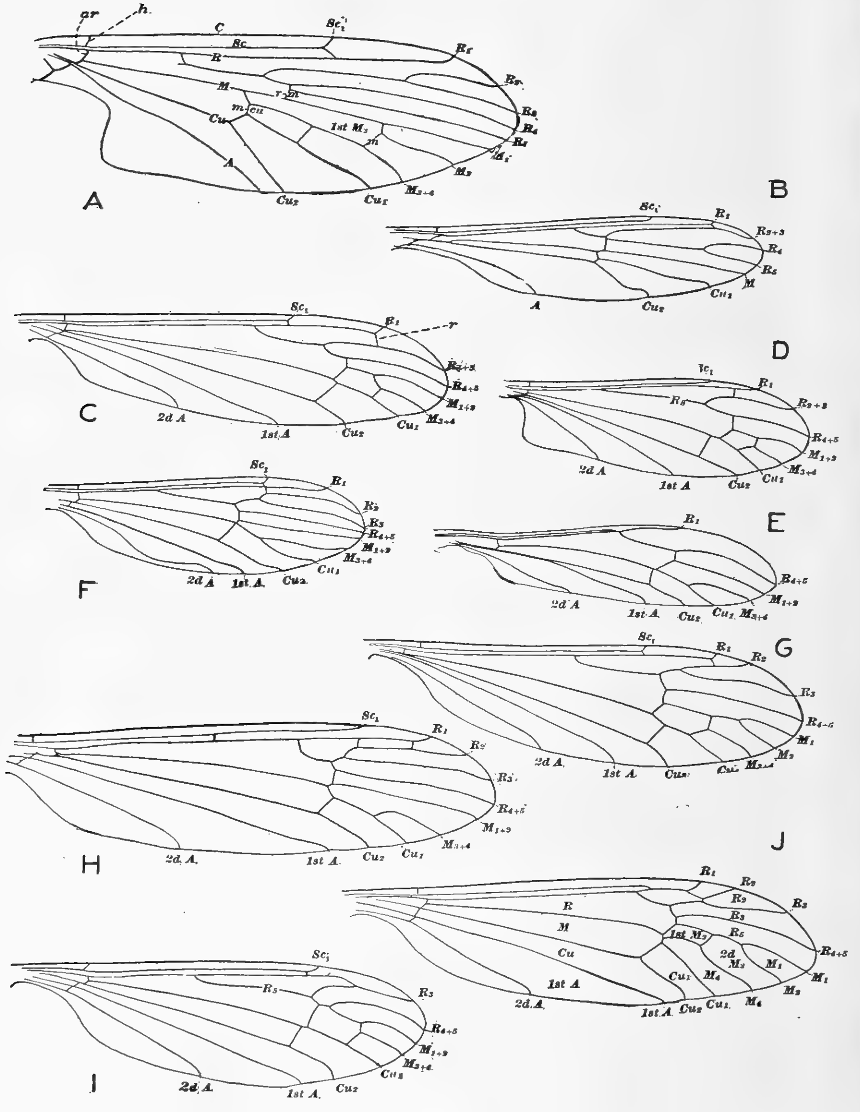


FIG. 128. WING VENATION

A, *Protoplasa fitchii.* B, *Bittacomorpha clavipes.* C, *Dicranomyia pubipennis.* D, *Antocha saxicola.* E, *Toxorhina muliebris.* F, *Erioptera septemtrionis.* G, *Limnophila subcostata.* H, *Dicranota rivularis.* I, *Liogma nodicornis.* J, *Tipula unifasciata*

most Limnophilini (Plates XXXVIII–XLI), or it may tend to retreat proximad toward the base of the wing as in many Eriopterini (Plates XXXIV–XXXVII), or it may be very far removed from the tip so that it lies before the base of the sector (as in the tribe Pekiciini, Plates XLI, XLII, and in the genus Ula, Plate XLI, 164). In some Antochini it is apparently lost by atrophy. In the subfamily Tipulinae only the more generalized species retain Sc_1 (Plate XLIII, 188 and 189), but Sc_2 is present and is bent strongly into R_1 at its tip, thus forming a good subfamily character.

The *radius* (R, fig. 128, A) is the strongest vein of the wing, and, with its sector, one of the most plastic. R_1 runs straight to the wing margin, but usually at about midlength of the wing it forks, sending off the radial sector (Rs). This is primitively twice forked, being forked and the branches forked again, dichotomously. These branches of the sector are numbered from 2 to 5, the upper fork carrying with it R_2 and R_3 and the lower fork carrying with it R_4 and R_5. The full complement of branches of the radial sector is found only in the Tanyderidae (Plate XXX, 1). In the Ptychopteridae (Plate XXX, 2–4) the upper fork, R_{2+3}, is fused to the margin; in the Tipulidae (Plates XXX–XLVIII) it is almost always the lower of the dichotomous forkings, R_{4+5}, that is fused to the margin.

The various ways in which the full complement of veins has been lost, by the fusing together of adjacent veins or else by the atrophy or dropping out of one or more of the branches, may be here discussed. In the Cylindrotominae (Plate XXX, 5–8) the appearance suggests the fusion of the upper fork of the sector (R_{2+3}) with R_1, forming a long, backward fusion of R_{1+2+3} from the wing margin. As suggested by the author in an earlier paper (Alexander, 1914 b:604–605) and later proved by the discovery of the Oriental genus Stibadocera Enderlein (Alexander, 1915 c: 178–179), the loss of these veins is by atrophy rather than by fusion, and the vein that simulates R_{1+2+3} is, in reality, R_3 alone and corresponds exactly to this vein in other tribes of crane-flies. In the subgenus Leiponeura of the genus Gonomyia (Plate XXXVI, 86–88), the vein R_{2+3} is fused to the wing margin, or, possibly, R_3 is atrophied after the fusion has proceeded almost to the margin. In the more generalized species of Gonomyia (Plate XXXVI, 89 and 90), the fork of R_{2+3} is

relatively deep, but it gradually becomes shallower until in such forms as *G. sulphurella* (Plate XXXVI, 91) it is very small and only a step removed from the condition obtaining in the subgenus Leiponeura. The venation in the genus Cladolipes, of the tribe Hexatomini, is similar. The genus Paratropeza of the tribe Antochini is the only member of that tribe with R_2 and R_3 separate at the wing margin, and in keys to the Tipulidae this genus runs down to the Eriopterini; the species are all exotic and are evidently the most generalized members of this aberrant tribe. In a few species of Gonomyia related to *G. blanda* (Plate XXXVI, 89 and 90), R_2 is very close to R_1 at the wing margin, in some cases being actually fused with it; this is likewise the condition in the Neotropical group Psaronius, where the fusion is most emphatic. The fork of R_{2+3} is often very deep, this cell being in many instances sessile or with R_2 even retreated back onto the radial sector (as in Molophilus, Plate XXXIV, 65–70; Tricyphona, Plate XLII, 178–185; *Limnophila emmelina*, Plate XL, 151; Rhaphidolabis, Plate XLI, 172–174), in which cases the anterior branch of the sector is simple and the posterior branch is forked, as in the Ptychopteridae already mentioned. These shiftings of the elements of the fork of the radial sector have been critically studied by Needham (1908). The radial cross-vein apparently is lost only by atrophy; the Cylindrotominae, discussed above, which appear to lose this vein by the fusion upon it of adjacent veins, in reality have it present and elongated, but simulating a section of vein R_1. In Eurhamphidia and Rhampholimnobia, of the East Indies, the fork of the radial sector occurs far beyond the line of the cord, while in most other crane-flies it is before or at this line. The radial-medial cross-vein (*r-m*) is usually present, but if lacking it is accounted for, apparently, only by the fusion of R_{4+5} on M_{1+2} (fig. 128, I); this fusion may be slight or extensive, and occurs in scattered genera in all the subfamilies of the Tipulidae. The radial-medial cross-vein lies distad of the medial cross-vein in Conosia and in some species of Rhamphidia. In many Dolichopezini (Plate XLIII, 186 and 187), Tipulini (Plate XLVIII, 247 and 248), and Cylindrotominae (Plate XXX, 5–8), the whole tip of R_2 is atrophied. In the remarkable genus Toxorhina (Plate XXXIII, 45 and 46), the radial sector is unbranched but the branch that persists is undoubtedly R_{4+5} alone, R_{2+3} having retreated back toward

the base of the sector and finally being lost by atrophy or by fusion with R_1; the exotic genus Ceratocheilus shows this intermediate condition very remarkably, and indicates clearly the manner in which this extreme reduction of the sector in Toxorhina was brought about.

The *media* (M, fig. 128, A), or medial vein, like the radial sector, in the hypothetical type of an insect wing is twice dichotomously forked, the closed cell, *1st* M_2, lying in the first fork. There are no known crane-flies that show this condition except the doubtful fossil genus Rhabdinobrochus, which is apparently based on an abnormal and imperfectly preserved specimen, and occasionally freak specimens of Tipula which indicate this condition by spurs of varying length. These specimens show that the single posterior branch of the media which persists is M_4, the spur always lying on the cephalic side and representing the atrophied M_3. Comstock (1918:349, fig. 360) has interpreted the venation of *Protoplasa fitchii* as showing all four branches of media, M_4 being fused with Cu_1 distally. That this is not the true interpretation is indicated by a study of the other species of Protoplasa. The vein in cell M_3 which Comstock interprets as being the downward deflection of M_4 is a supernumerary cross-vein. In this remarkable family of flies, such cross-veins are very often found in different cells of the wings. That the presence of a vein in cell M_3 is a specific character only is shown by the fact that it is lacking in the related *Protoplasa vipio* O. S. M_1 and M_2, comprising the anterior fork of the vein, are either separate or fused at the wing margin; such genera as Limnophila (Plates XXXVIII–XL) show a perfect succession, from deep forks as in the exotic *Limnophila epiphragmoides* (Alexander, 1913 b:543), thru less deep forks as in *L. montana* (Plate XL, 148), to *L. brevifurca* (Plate XXXVIII, 125), which has a very shallow fork that is sometimes fused clear to the wing margin, and further to the numerous species of the genus (Plate XL, 150–157) in which there is a permanent and constant fusion between these veins extending entirely to the wing margin and obliterating the cell M_1. In all except the most generalized species, including nearly all of the Limnobiinae, the medial-cubital cross-vein (*m-cu*) is obliterated by the fusion of M_{3+4} with the upward deflection of Cu_1; this fusion may be short or long, and is discussed in connection with the cubitus. After breaking away from the cubitus, M_3 generally runs free to the wing margin, but in some cases (as in Styringomyia and Phalacrocera, Plate XXX, 8 and 9) it

unites with M_{1+2} for a short distance, obliterating the medial cross-vein. In some genera — Bittacomorpha (Plate XXX, 3), Bittacomorphella (Plate XXX, 4), Hexatoma (Plate XXXVII, 112), Diotrepha, and many species of Trentepohlia — but one branch of the media reaches the wing margin, and in these cases the posterior branch has either fused with the cubitus (as in Hexatoma) and reaches the margin by this fusion, or has been lost by atrophy. Needham (1908:227–229) believes the posterior branch of the media is lost only by atrophy, and undoubtedly this is true in most instances; the series of Polymera, however, a tropical, American genus studied by the author (Alexander, 1913 b:526–535), showed an interesting condition indicating that the veins may be united by fusion, and similar conditions may exist in the genus Rhaphidolabis and in the South African species *Gonomyia brevifurca*. The entire end of M_3 is lost by atrophy in four known species of Dicranomyia, one of these being *D. whartoni* (Plate XXXI, 15). The cell *1st* M_2 (discal) is in many cases opened by the atrophy of part of M_3, leaving the tip of M_3 attached to the medial cross-vein (as in Ormosia, Plate XXXIV, 59–64, and in Gonomyia, Plate XXXVI, 92 and 93); in other cases it is the medial cross-vein (*m*) that is atrophied, opening the cell (as in Dicranomyia, Plate XXXI, 14 and 16, in Cryptolabis, Plate XXXVII, 101, and in many genera of the Pediciini, Plate XLI, 172–174).

The *cubitus* (*Cu*, fig. 128, A), lying between the media and the anal veins, is the most constant and, after the radius, the most powerful vein of the wing. There are always two branches, which are never lost. At the fork, the anterior branch, Cu_1, is directed strongly forward, so that in all but the most generalized forms it simulates a cross-vein and from its conspicuous size it has long been termed the *great cross-vein*; this deflection is the basal deflection of Cu_1 of the Comstock-Needham system, and the *pars ascendens* of Bergroth. In the more generalized groups, such as Tanyderidae (Plate XXX, 1), Ptychopteridae (Plate XXX, 2–4), a very few Limnobiinae — as some species of Tricyphona (Plate XLII, 184 and 185) — and many of the Tipulinae (Plate XLIII, 195–197), the medial-cubital cross-vein (*m-cu*) is persistent, but in the great majority of cases it is lost by the fusion of Cu_1 and M_{3+4}. As already stated, this fusion may be very short — merely a point of contact (punctiform), as in most species of Tipula (Plate XLVI, 222) — or it may be subequal in length to the cell *1st* M_2, the deflection of Cu_1 entering the media at

its fork and breaking away from M_3 at the distal end of the cell; this long fusion with M_3 is the rule in the subfamily Limnobiinae, but is very unusual in the Tipulinae, the South African genus Leptotipula being almost the only instance known. In some groups the deflection lies far before the fork of the media, as in the transient fusions of Nephrotoma (Plate XLIV, 198 and 202) and Dolichopeza (Plate XLIII, 187) or the longer fusions of many Gonomyia (Plate XXXVI, 89 and 90) and other genera. In the highly specialized condition obtaining in Orimarga and even more accentuated in the tropical-American genus Diotrepha, the deflection of Cu_1 is retreated far toward the wing base, so that in the latter genus the fusion of Cu_1 with M is about half the length of the entire wing. On the other hand, Cu_1 may unite with M_3 far out toward the tip of the wing, (as in Trichocera, Plate XLI, 165 and 166), so that Cu_1 extends beyond M and is connected with it by the *m-cu* cross-vein, which here runs longitudinally and simulates a section of one of the longitudinal veins. In the great majority of crane-flies, the fork of the cubitus is so deep that the branch Cu_2 is longer than the deflected part of Cu_1; in some species of Limnophila (Plate XXXVIII, 113), however, and also and especially in the tribe Hexatomini (Plate XXXVII, 104 and 105), the condition is usually reversed and it is Cu_2 that is the shorter element of the fork. Cu_2 is usually free at the wing margin, but in most Old World species of Trentepohlia and in one species of Dicranomyia it is fused with the first anal vein for a varying distance back from the tip.

The *anal veins* (*1st A*, *2d A*, fig. 128) comprise in the generalized wing three simple veins, as apparently shown in the fossil genus Cladoneura; a single anal vein is found in the Ptychopteridae and in most of the Tanyderidae, and there are two in all the Tipulidae and in the fossil tanyderid genus Etoptychoptera Handlirsch. The anal veins are simple in all native forms; the second one is forked in the South African genus Podoneura, in some species of Styringomyia, and in abnormal specimens of Helobia. As indicated by Needham (1908), if the second anal vein found in Helobia (Plate XXXVII, 98) and that in Trichocera (Plate XLI, 165) were united, the condition would be remarkably like what is found in Podoneura, and the condition in these genera may have been brought about by the loss of the anterior branch of the fork in Trichocera and the posterior branch in Helobia. In the Tipulini and some other tribes there is a strong vein lying close beneath Cu and often quite removed

from it. This probably represents the first anal vein in these species, in which case all three anal veins would be accounted for.

The cross-veins.— The usual cross-veins of the wing have been indicated, for the most part, in the foregoing discussion of the longitudinal veins. The humeral cross-vein (h) is almost always present and forms a strong union between C and Sc near the wing base; it is of little systematic importance. The radial cross-vein (r) lies entirely in the radial field, and connects R_1 with either R_2 or R_{2+3}, or it may lie exactly at the fork of the last-named vein. The radial-medial (r-m) cross-vein connects either R_{4+5} with M_{1+2} as in most crane-flies, or R_5 with M_{1+2} as in Molophilus (Plate XXXIV, 65–70), or Rs with M_{1+2} as in *Tricyphona kuwanai* of Japan and in the genus Rhampholimnobia discussed above. The medial cross-vein (m) lies entirely in the medial field and connects either M_2 or M_{1+2} with M_{3+4}. The medial-cubital cross-vein (m–cu) connects either M or M_{3+4} with Cu_1. The arculus (ar) is a strong cross-vein connecting M with Cu at the base of the wing.

Supernumerary cross-veins and spurs are frequently found in crane-flies and furnish convenient characters for defining genera, subgenera, and species. In *Tanypremna regina,* of the Colombian Andes, there is an abundance of cross-veins and spurs in the basal cells of the wings; in the related species *Tanypremna columbiana* there is a single strong cross-vein in cell M. These supernumerary cross-veins are very constant in their occurrence and position, and may be found in almost any cell of the wing. Needham (1908:220) drew a primitive crane-fly wing and indicated on it all the supernumerary cross-veins that are known to occur in the group, and the composite resulting was remarkably like the wing of a neuropteroid scorpion fly, thus providing additional confirmation for the belief that the Panorpidae or some closely allied group gave rise to the dipterous line of evolution. Epiphragma (Plate XLI, 158) has the cross-vein in cell C; Geranomyia (Plate XXXI, 10–13) and many Rhipidia in cell Sc; Helobia (Plate XXXVII, 98) and Dicranophragma (Plate XXXIX, 139) in cell R_2; Ephelia (Plate XXXIX, 137 and 138) and Idioptera (Plate XXXVIII, 115) in cell M; Dicranota (Plate XLI, 167–169) in cell R_1, alongside of the r cross-vein; Discobola (Plate XXXII, 41) in the first anal cell, forming a strong union between the two anal veins; and so on in great variety. Strong spurs are frequently found at the origin of the radial sector (Plate XXXVIII, 115 and 116), or in a

few cases in other parts of the wing, as in Hoplolabis (Plate XXXV, 83), where a strong spur juts into cell *1st* M_2 from its outer end.

Adventitious cross-veins, or veins which are inconstant and of sporadic occurrence within a species, being in some cases present in one and absent in the other of the two wings of a single individual, are rather frequent in the Tipulidae, the most notable cases being the genus Cladura (Plate XXXVII, 102) as noted by Alexander and Leonard (1912), and the species *Tricyphona inconstans* (Plate XLII, 177) as noted by Johnson (1901).

The cells.— The cells of the wing take their names respectively from the veins lying immediately before or above them; in the case of fused veins the cell takes its name from the last element of the fusion. Thus the cell behind vein R_3 is cell R_3, that behind vein M_1 is cell M_1, that behind vein R_{4+5} is cell R_5, and so on (fig. 128, J). When the cells of a field are cut by cross-veins, either primary such as r and m or supernumerary, the proximal cell is the first and the distal cell is the second. Thus in many crane-flies the discal cell is present, being cut off by the m cross-vein at its outer end; and since both cells lie behind vein M_{1+2}, both are cell M_2, the proximal cell (discal) thus becoming *1st* M_2 and the outer cell becoming *2d* M_2. The same thing is true of the cell R_1, which in some cases (as in Dicranota, Plate XLI, 167–169) is divided into three cells, numbered outward from the proximal (*1st* R_1) to the distal (*3d* R_1). In most cases the wing cells lying proximad of the arculus are so small and reduced that they cannot be readily homologized; but in the tropical-American genus Peripheroptera they attain a remarkable development, occupying in the males of some species from one-third to one-half of the entire wing length. The anal angle of the wing is variously developed, being usually prominent in the family Tanyderidae (Plate XXX, 1), the genus Antocha (Plate XXXIII, 48), and the subgenus Sacandaga of the genus Rhabdomastix (Plate XXXVI, 97), and on the other hand being lacking or nearly so in some exotic Limnobiini, such as Thrypticomyia and the males of Peripheroptera.

The stigma.— The stigma is a dark spot or area usually situated near the end of vein R_1 and often bisected by the radial cross-vein. It may be either present or lacking in the various species of a genus, and in some cases is very large and pubescent, as in the males of the genus Empedomorpha Alexander.

The abdomen

The abdomen, the third and last region of the body, lies behind the thorax and is attached to the caudal parts of the metathorax. It is composed of nine apparent segments, or annuli, numbered from the basal (first) to the terminal (ninth). Each of these segments consists of three regions — a dorsal sclerite, the *tergite*; a ventral sclerite, the *sternite*; and a lateral region on either side, the *pleurites*, these being either integumentary or chitinized. The abdominal spiracles are located in this pleural conjunctiva. There is but little modification of the general type in the various groups of crane-flies.

The first segment is very short and appears as a narrow ring closely attached to the metathorax; the second is the longest of the segments; the remaining segments are subequal in size, or, in the male sex especially, shortened and crowded toward the end of the abdomen. In many species of Tipulinae there are present on the abdominal segments rectangular areas of impressed punctures on either side of the median line, which on the second tergite are about midlength of the sclerite and on the succeeding tergites are on the basal part; often there are smaller areas of punctures nearer the caudal margin of the sclerites. These areas are usually present on the sternites as well as on the tergites. The sexual organs are borne at the end of the abdomen in both sexes.

The male hypopygium. — The hypopygium, or propygium, of the male sex is of extreme importance in the determination of species. In many groups and genera (Gonomyia, Molophilus, Tipula, and others) it is almost impossible to identify the species without considering the details of structure of the male genitalia, and in these groups the hypopygium is of paramount importance in specific determination.

The structure of the hypopygium is relatively uniform and homologous thruout the crane-fly series. The organ has been discussed in considerable detail by previous authors, especially by Snodgrass (1904), whose terminology is adopted in this paper. The European authors still adhere largely to the cumbersome terminology of Westhoff (1882).

In the generalized species the hypopygium shows but little complexity and enlargement, the terminal segments of the abdomen being of approximately the same size and diameter as the preceding segments. In the specialized species of many genera (Gonomyia, Limnophila, Tipula,

and others), the hypopygium is enlarged and complicated in structure, the enlargement often involving the terminal two or three segments. The modifications of the eighth and ninth segments are almost inconceivable in their variety, and only the more important types can be mentioned here.

The Tipulinae: In the tipuline forms the pleura are intimately attached to the sternites, and their appendages lie parallel to each other,

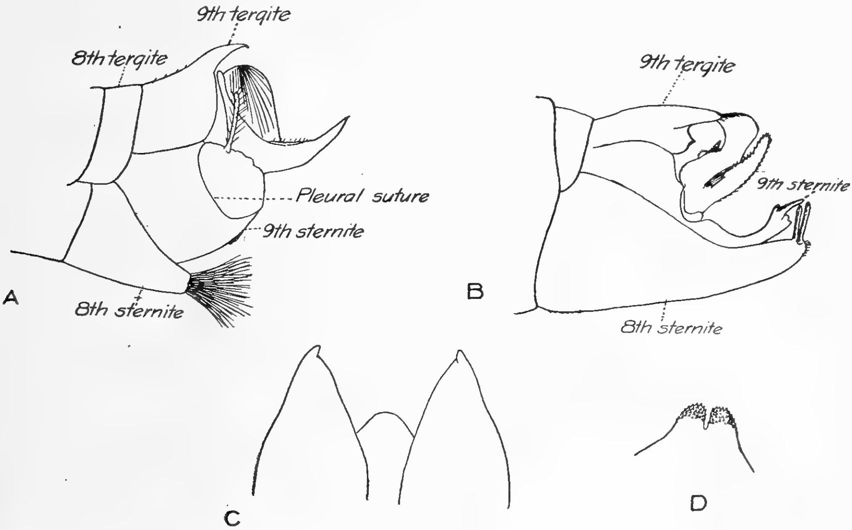


FIG. 129. MALE HYPOPYGIUM, TIPULINAE

A, *Tipula monticola,* lateral aspect. B, *T. parshleyi,* lateral aspect. C, *T. monticola,* ninth tergite, dorsal aspect. D, *T. sulphurea,* ninth tergite, dorsal aspect

work longitudinally, and act as claspers by jutting into the notch of the ninth tergite.

The ninth tergite (fig. 129, C and D) is the terminal dorsal plate of the abdomen. It is of various shapes, but usually rectangular, and may be very large or correspondingly reduced. The caudal margin is variously modified (Plates XLIX–LII), being in some cases nearly straight across and in others notched by V- or U-shaped incisions, with the lateral lobes often produced into long-extending arms, and the appendages of the ninth pleurite jutting into the notch in a position of rest. In some cases the

caudal margin is produced into a strong median lobe (Plate L, 287), or into two slender lobes (Plate XLIX, 271 and 272), one on either side of the median line. The writer regards the ninth tergite as offering the surest and easiest characters for identifying the species of Tipula, and its various forms are accordingly illustrated in this paper.

The ninth sternite may be either prominent or insignificant. It bears on its caudal part the ninth pleurites, or pleural region. In primitive forms the pleurites are distinct, being cut off by the *pleural suture* (fig. 129, A); in other forms the suture is obliterated to a greater or less degree and the pleural region is thus immovably attached to the sternite. In very many Tipulinae (as in most species of Nephrotoma and many species of Tipula), the pleural suture is represented only by a short, curved impression on the ventral side of the fused ninth sterno-pleurite. In the genus Longurio the ninth sterno-pleurite is exceedingly elongated, the pleural region being situated at the caudal end and bearing at its apex the pleural appendages, which, in a position of rest, lie in the dorsal concavity of the elongate sterno-pleurite. In some species — *Tipula parshleyi* (fig. 129, B, and Plate LV, 354), *T. trinidadensis*, *T. macrosterna*, *T. gladiator*, and others — it is the eighth sternite that is so greatly enlarged, the ninth sternite being comparatively small and often lying in the dorsal concavity of the eighth sternite. The ninth sternite is usually more or less incised on the mid-ventral line by a deep notch, which in some cases seems to bisect it; such deep notches are spoken of as *profound incisions.*

The only paired element of the hypopygium consists of the ninth pleurites, there being one pleurite on either side of the organ. Usually the pleurites are small and oval, but in some cases they are greatly produced, as in *Tipula macrolabis* and *T. macrolaboides* (Plate LIII, 322 and 323); in other species they are curiously twisted and semi-coiled, as in *T. streptocera;* while in many species an intermediate condition is found in which the pleurite is produced in a moderate degree only (as in *T. loewiana*, *T. mandan*, and others). The pleural appendages are usually two in number. The outer one is more or less fleshy and is of various shapes and sizes in the different groups. In the genus Nephrotoma it is broadly oval to elongate-oval and usually pointed, in many species the tips being greatly produced and attenuated. In the genus Tipula it may be very tiny, cylindrical, and tending to be reduced, as in the

bicornis group (*Tipula parshleyi, T. morrisoni, T. bicornis, T. megaura, T. johnsoniana*); moderate in size and more or less cylindrical, as in the *valida* group (*T. valida, T. hirsuta*) and the *umbrosa* group (*T. umbrosa, T. monticola, T. triton, T. mingwe, T. tuscarora*); or broad, rectangular, and very flattened, as in the *oleracea* group (*T. perlongipes, T. kennicotti, T. sulphurea*) and the *tephrocephala* group (*T. tephrocephala, T. cayuga*). The inner pleural appendage varies in shape, but usually it has a heavily chitinized, split apex jutting cephalad into the notch of the ninth tergite.

The penis guard and the gonapophyses vary in size and shape. In some species, as *Tipula tuscarora*, they are small and shaped like a trident; in other species (*T. triton, T. johnsoniana*) the gonapophyses are very large and prominent, and subtend the penis guard. The central vesicles from which the penis arises are often very large. In many species the penis is very long and slender, and when exserted is equal to half the length of the entire abdomen.

In many species the eighth sternite is not at all produced and is unarmed (*Tipula angustipennis, T. senega, T. serta, T. perlongipes, T. kennicotti, T. sulphurea*); in other species it is provided with prominent chitinized spines on either side, which are decussate (*T. tuscarora*, Plate LIII, 328), or with large to small tufts of silvery hairs on either side of the median line, these often surrounding one or two small bristles (*T. monticola, T. triton, T. mingwe, T. submaculata*), or with fleshy lobes (*T. australis*, Plate LIII, 326, *T. umbrosa, T. valida*). In the generalized members of the South American *monilifera* group (*T. exilis, T. andalgala*, and others) the sternite bears a prominent tripartite appendage.

In several species the ninth tergite is fused with the ninth sterno-pleurite so that the entire ninth segment forms a continuous ring, as in *Tipula ultima* (Plate LIII, 333), *T. perlongipes, T. kennicotti, T. sulphurea*.

The Limnobiinae: In the limnobiine forms the pleurites are prominent and have their appendages elevated above the level of the ninth sternite and the ninth tergite; these appendages are very often decussate or contiguous, work transversely across the genital chamber, and act as claspers by direct, pincer-like contact. In the genus Geranomyia (fig. 130, A) and others, the ventral pleural appendages are generally soft and fleshy, and the dorsal pleural appendages are sharp, more or less curved, chitinized hooks. In Gonomyia (fig. 130, B) the appendages are very complex in the

specialized forms, and are difficult to homologize even in species that are unquestionably closely related. This condition occurs in several other groups, as in the mycetophilous genus Sciophila and related groups, according to Dr. Johannsen, who has studied the family. In Acyphona and other genera the hypopygium is asymmetrical in relation to the remainder of the abdomen, the ninth abdominal segment being twisted half around. In some limnophiline forms (Phyllolabis, Oromyia, *Limnophila mundoides*) the hypopygium is enlarged and complex, suggesting the condition found in many species of Tipula; in Phyllolabis the eighth

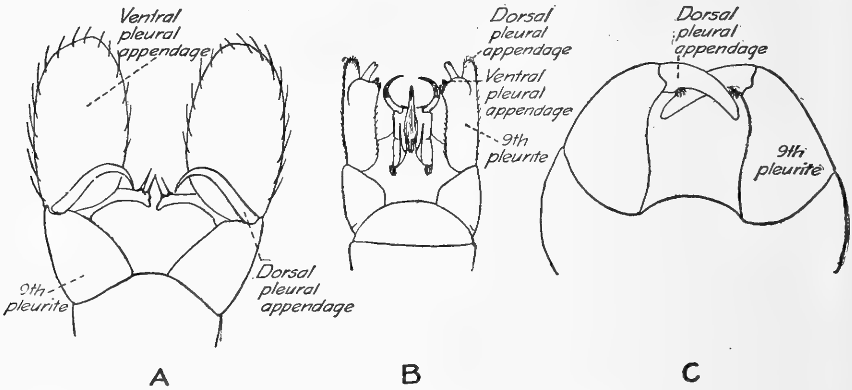


FIG. 130. MALE HYPOPYGIUM, LIMNOBIINAE

A, *Geranomyia rostrata*, dorsal aspect. B, *Gonomyia amazona*, ventral aspect. C, *Chionea primitiva*, dorsal aspect

sternite bears a pale foliaceous appendage, while in Oromyia the ninth sternite is produced into a conspicuous lyriform plate. In Chionea (fig. 130 c), Cladura, and Pterochionea, there is a single powerful pleural appendage on each side.

The normal type of structure in the Limnobiinae consists of short to elongate pleurites, bearing at or near the apices two or three appendages which are usually chitinized and decussate in a position of rest. The penis guard occupies the ventral area of the genital chamber, the anal tube the dorsal area.

The female hypopygium.— The female hypopygium, or ovipositor, is characteristic in many species of the Tipulidae. In most cases it consists

of four horny or chitinized pointed valves, which are paired — there being two dorsal (*tergal*) and two ventral (*sternal*) valves. These valves are often acicular and are used for the insertion of the eggs in oviposition. In most species they are curved upward so that the concavity is on the dorsal side, but in the genus Trichocera (fig. 131, A) and some of its near allies the ovipositor bends downward, the concavity being on the ventral side.

As wide a range in structure of this usually homogeneous organ as occurs in the group, is found in the genus Tipula. The tergal valves

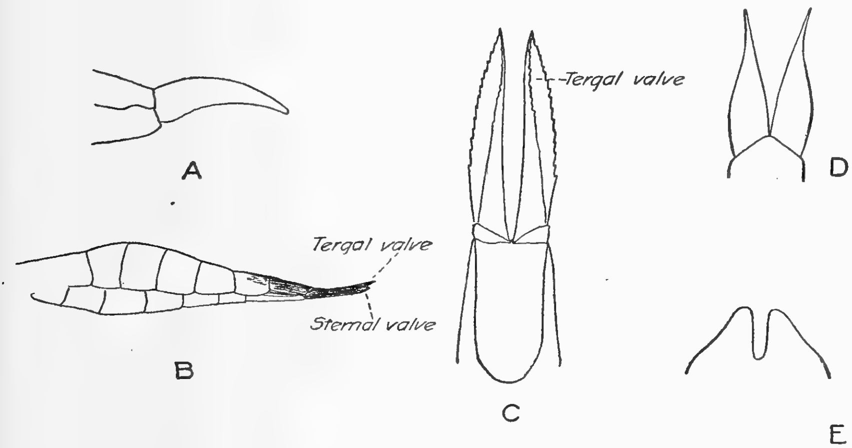


FIG. 131. FEMALE HYPOPYGIUM, OR OVIPOSITOR

A, *Trichocera bimacula*, lateral aspect. B, *Tanyptera frontalis*, lateral aspect. C, *Tipula longiventris*, dorsal aspect. D, *Tipula piliceps*, dorsal aspect. E, *Tipula parshleyi*, dorsal aspect

are usually longer than the sternal valves (fig. 131, C), and both tergal and sternal valves assume a variety of shapes. They are often slender to subacicular; the tergal valves may be sharply serrated on their outer faces, as in many Arctic and North Temperate species — *Tipula arctica*, *T. longiventris* (fig. 131, C), *T. labradorica*, *T. serricauda*; all the valves may be short and fleshy, superficially resembling the male genitalia but being smaller — as in the Cylindrotominae and Styringomyiini, and in *Tipula bicornis*, *T. megaura*, *T. parshleyi* (fig. 131, E), *T. morrisoni*, *T. nobilis*, and other species; all the valves may be short and truncated across their tips but strongly chitinized, as in *Tipula mandan*; or the sternal

valves may be very much reduced, as in *Tipula serricauda.* The ovipositor in Tanyptera (fig. 131, B) is normal, but the terminal abdominal segments are greatly narrowed and produce a saber-like appearance.

SEXUAL DIMORPHISM

Besides the differences between the two sexes in the shape of the antennal segments, already discussed, there are many other structural differences. In some species the eyes of the female are much smaller than those of the male, and in the latter the eyes may be contiguous (*holoptic*) or approximated. In species with elongated rostra, such as in the genus Geranomyia, the rostrum of the female is often much shorter than that of the male. The legs of the female are in some cases shorter than those of the male. The wings of the females of many species in widely separated tribes are often reduced so as to be incapable of flight; in some forms (Empedomorpha) the stigma of the male is much larger than that of the female; in *Tipula armatipennis* of southern Brazil, the wing of the male is armed with an acute spur above the stigma; many other species have the costal region strongly incrassated; in the genus Peripheroptera, with the greatly enlarged cells before the arculus described elsewhere, these cells are much smaller in the female than in the male, and the anal angle of the wing is more prominent.

Color dimorphism is found in the species of Ctenophora and Tanyptera, the specific limits of which are very poorly understood at present. In at least three eastern-American species of Tipula (*Tipula fuliginosa, T. annulicornis,* and *T. taughannock*), the males are light yellow, while the females are from dark brown to brownish black and appear to be very different insects.

As a rule the females are larger than their mates, but in some species (Teucholabis, *Eriocera longicornis,* and others) the male sex is the larger.

HAUNTS

The various species of Tipulidae are, within rather broad limits, confined to certain definite haunts or ecological situations. Some species are very closely restricted by their habitat, while others occur in a great diversity of situations. There is no crane-fly that can be called cosmopolitan; *Helobia hybrida* is nearly so, ranging, as it does, over most of the New World, the Palaearctic region, and southward into the Oriental

region. *Conosia irrorata* is another wide-ranging species, being found in almost all of eastern Africa, in southern Asia as far north as Japan, and thence eastward to Australia. *Nephrotoma ferruginea*, one of the commonest of the local forms, ranges over the whole North American continent. The majority of species, however, have a very much more restricted range, the crane-fly fauna of eastern America being largely confined to that region, while the crane-flies found west of the Rocky Mountains are almost all distinct from those of eastern America. Natural barriers, such as large bodies of water, deserts, and mountains, serve to limit and restrict the range of the species.

The presence of moisture is almost a necessity in crane-fly development, and consequently the species as adults occur in the vicinity of water, either running, standing, stagnant, permanent, or temporary. No species confined to sandy or arid conditions are known to the writer, the nearest approach being in Helobia, Trimicra, and Empedomorpha. A few typical situations are here outlined and the more constant inhabitants of these haunts listed:

1. Species inhabiting swampy (helophytic) situations: either grass swamps with little woody elements entering in — *Dicranomyia longipennis, Erioptera graphica, E. parva, Stygeropis fuscipennis, Tipula sayi, T. tricolor*; or bush swamps with a certain shrubby element such as Alnus, Spiraea, and the like — *Bittacomorpha clavipes, Ptychoptera rufocincta, Adelphomyia cayuga, Limnophila fasciolata, Rhamphidia mainensis, Tipula dejecta, T. sulphurea, Tricyphona inconstans, T. paludicola.*

2. Species inhabiting wet meadows or grasslands, and found along the (usually) grassy banks of streams not necessarily in deep shade — *Protoplasa fitchii, Geranomyia canadensis, G. rostrata, Antocha saxicola, Toxorhina muliebris, Rhamphidia flavipes, Atarba picticornis, Erioptera chlorophylla, E. straminea, E. vespertina, E. caloptera, E. armata, E. venusta, Gnophomyia tristissima, Gonomyia sacandaga, G. alexanderi, G. sulphurella, G. cognatella, G. subcinerea, G. noveboracensis, G. mathesoni, Rhabdomastix flava, Cryptolabis paradoxa, Epiphragma fascipennis, Limnophila macrocera, L. unica, L. tenuipes, L. recondita, L. imbecilla, L. luteipennis, L. inornata, L. quadrata, L. lenta, L. noveboracensis, Hexatoma megacera, Eriocera fultonensis, E. longicornis, Nephrotoma ferruginea, N. incurva, N. pedunculata, N. tenuis, N. xanthostigma, N. eucera, Tipula angustipennis, T. bella, T. caloptera, T. strepens, T. eluta, T. fraterna, T. cunctans, T. bicornis, T. parshleyi, T. tephrocephala, T. umbrosa.*

3. Species living under bog conditions (oxylophytic), in proximity to Sphagnum — *Limnophila laricicola, Phalacrocera tipulina.*

4. Species inhabiting rocky (lithophytic) situations, usually clinging to the vertical faces of cliffs, hiding in crevices of the rocks, or resting on vegetation growing in such haunts — *Bittacomorphella jonesi, Geranomyia canadensis, G. diversa, Dicranomyia badia, D. stulta, D. simulans, Limnophila montana, Tricyphona auripennis,* Oropeza, *Dolichopeza americana, Tipula macrolabis, T. senega*; the species of Oropeza and Dolichopeza also lurk beneath dark bridges and under culverts.

5. Species inhabiting open gorges, found on the usually luxuriant vegetation of the talus slopes and along the floor of the ravines — *Dicranomyia monticoloides, D. monticola, Geranomyia diversa, Limnophila cubitalis, Adelphomyia minuta, Ula elegans, Tipula collaris, T. senega, T. taughannock, T. fuliginosa, T. valida.*

6. Species inhabiting shaded, cold Canadian woodlands (mesophytic), usually found on rank vegetation in the shade of hemlock, beech, yellow birch, sugar and red maples, and the like; they occur in close proximity to water, on herbage such as ferns, horsetails, Taxus, Streptopus, Clintonia, Smilacina, Medeola, Laportea, Coptis, Dalibarda, Impatiens, and Viola, from which they may be swept with a net — *Dicranomyia immodesta, D. gladiator, D. halterata, D. pubipennis, D. globithorax, D. macateei, Rhipidia maculata, Limnobia solitaria, L. indigena, L. parietina, L. triocellata, L. tristigma, Elephantomyia westwoodi, Toxorhina muliebris, Dicranoptycha germana, Atarba picticornis, Ormosia apicalis, O. monticola, Erioptera armillaris, E. megophthalma, E. stigmatica, E. nyctops, Molophilus pubipennis, M. fultonensis, M. hirtipennis, M. comatus, M. ursinus, Gonomyia florens, G. blanda, Cladura delicatula, C. flavoferruginea, Limnophila albipes, L. niveitarsis, L. tenuicornis, L. toxoneura, L. areolata, L. adusta, L. nigripleura, L. subcostata, L. alleni, L. brevifurca, L. aprilina, L. johnsoni, L. fuscovaria, L. rufibasis, L. munda, L. sylvia, L. stanwoodae, L. osborni, L. noveboracensis, L. emmelina, L. edwardi, Adelphomyia americana, A. minuta, A. cayuga, Ulomorpha pilosella, Pedicia albivitta, P. contermina, Tricyphona vernalis, T. katahdin, T. calcar, Rhaphidolabis rubescens, R. tenuipes, R. flaveola, R. modesta, Cylindrotoma americana, C. tarsalis, Liogma nodicornis, Longurio testaceus, Tipula oropezoides, T. algonquin, T. senega, T. hermannia, T. fragilis, T. macrolabis, T. mingwe, T. monticola, T. hirsuta, Trichocera bisinuata, Bittacomorphella jonesi.*

7. Species inhabiting shaded Transitional woodlands (mesophytic), often quite open, in shade of hornbeam, basswood, hickory, butternut, ash, and other trees, usually near running water, occurring on a variety of rank herbage and low vegetation such as Thalictrum, Podophyllum, Menispermum, Nepeta — *Dicranomyia immodesta, D. pudica, D. rostrifera, D. brevivena, D. liberta, D. haeretica, D. morioides, Rhipidia fidelis, Limnobia fallax, L. indigena, L. cinctipes, L. immatura, L. triocellata, Discobola argus, Rhamphidia flavipes, Dicranoptycha sobrina, D. winnemana, Atarba picticornis, Teucholabis complexa, Ormosia nubila, O. innocens, O. nigripila, O. rubella, O. meigenii, Erioptera septemtrionis, E. chrysocoma, E. chlorophylla, E. armata, Molophilus hirtipennis, M. pubipennis, Gonomyia alexanderi, G. sulphurella, G. cognatella, Cladura flavoferruginea, Limnophila macrocera, L. tenuipes, L. adusta, L. subcostata, L. ultima, L. fuscovaria, L. cubitalis, L. quadrata, L. lenta, Epiphragma fascipennis, Adelphomyia americana, Dicranota noveboracensis, D. rivularis, Rhaphidolabis cayuga, R. tenuipes, Nephrotoma ferruginea, N. incurva, N. lugens, N. macrocera, N. tenuis, Tipula unimaculata, T. angustipennis, T. senega, T. apicalis, T. strepens, T. hermannia, T. collaris, T. nobilis, T. grata, T. hebes, T. longiventris, T. morrisoni, T. taughannock, T. fuliginosa, T. submaculata, T. tephrocephala, T. ultima.*

8. Species found in the immediate vicinity of streams and rivers, on the rocks or on trees and bushes near by — *Dicranomyia immodesta, D. badia, D. stulta, D. morioides, D. simulans, Geranomyia diversa, G. canadensis, Antocha saxicola, Cryptolabis paradoxa, Hexatoma megacera, Eriocera brachycera, E. spinosa, E. longicornis, E. cinerea, E. fultonensis, E. tristis, Dicranota noveboracensis, D. rivularis, Tipula bella, T. caloptera, T. eluta, T. strepens.*

9. Species found in southern gum swamps, where the forest cover is largely bald cypress (Taxodium), sweet gum (Liquidambar), sour gums (*Nyssa aquatica* and *N. sylvatica*), and the like, and the herbage consists largely of lizard's-tail (Saururus) — *Gonomyia puer, G. manca, Limnophila recondita, L. luteipennis, L. irrorata, Penthoptera albitarsis, Eriocera wilsonii, Brachypremna dispellens, Tipula tricolor, T. perlongipes, Nephrotoma okefenoke, N. virescens.*

ACTIVITIES

Feeding habits

The species with elongate rostra (Geranomyia, Toxorhina, Elephantomyia, and others) feed on the nectar of tubular flowers, the Compositae being chosen by most of the species, at least in eastern America. Knab's

(1910) very valuable paper cites in detail the feeding habits of the local species of Geranomyia, which sip the nectar from various composite flowers (Eupatorium, Solidago, Aster, Erigeron, Silphium, Rudbeckia, Verbesina, Cacalia, and others). A few other plant families (Apocynaceae, Ericaceae, Umbelliferae, Rhamnaceae, Lauraceae) are fed upon by various species of crane-flies. The food of the majority of crane-flies, or, indeed, their duration of existence in an adult state, is very little understood. Many species are presumed to be comparatively short-lived and would not require food before the essential functions of reproduction and oviposition were completed; other forms, however, are on the wing for so long a time that it is probable that some sort of food is taken during this period.

Resting habits

The Tipulidae vary in their resting habits and in the positions assumed, according to the species and to the habitats frequented. Some (as Molophilus and Erioptera) rest on the vertical or inclined surfaces of trees, cliffs, or buildings, with all the legs far outstretched like those of a spider. Many others habitually rest on the upper or the lower surfaces of leaves. In such positions of rest the wings are usually held outspread, or divaricate, in the Tipulinae, and folded over the abdomen in the Limnobiinae. But such broad generalizations break down even within a single genus. Thus, in Limnophila such species as *munda*, *areolata*, and *niveitarsis* have the wings folded over the back, while *L. toxoneura* and the related *Epiphragma fascipennis* hold the wings divaricate; in the genus *Tipula*, most species of which rest with outspread wings, the species of the *marmorata* group (*fragilis*, *ignobilis*, and others), as well as those of the related genus Longurio, hold the wings incumbent over the abdomen. Some exotic crane-flies (as the genus Thrypticomyia, *Dicranomyia saltens*, and several species of Trentepohlia) habitually rest on spiders' webs. All these species have conspicuously white feet; *Dicranomyia saltens* has a curious horizontal dance along a transverse strand. Species of Dolichopeza and Oropeza living in caves and beneath dark culverts, hang suspended from the roof by one or two pairs of legs. *Limnophila montana*, *Dicranomyia badia*, *D. simulans*, and some other species that live on cliffs, rest flat against the rock with all the legs on the support. Many species of Limnobiini (*Geranomyia canadensis*,

G. diversa, Dicranomyia simulans, D. badia, D. stulta) practice a curious up-and-down bobbing while at rest or while feeding, their long, slender legs acting as springs.

Swarming and mating

Swarming usually takes place during the early hours of twilight or in the late afternoon. The swarming of the Limnobiinae is a familiar performance. The number of individuals participating varies from two or three to a dozen or twenty in *Rhabdomastix flava, Ula elegans, Limnophila brevifurca, L. ultima*, and *Epiphragma fascipennis*, several hundreds in most species of Ormosia and Erioptera, and vast swarms in species of Trichocera and in *Eriocera longicornis*, in which many thousands of individuals are involved. In practically all cases the start of the swarm is the same. It begins with one or two individuals and is gradually augmented by the arrival of newcomers. Usually the flight is not far above the ground, that of the smaller species (as in the genera Ormosia, Limnophila, Dicranota, and Rhaphidolabis) taking place under the low branches of a tree or the inclined trunk of a fallen log. In Eriocera, however, mating usually takes place in the open, often over the broad expanse of a river or a stream. The vertical height covered by the dance varies from a few inches in some species to many feet in *Brachypremna dispellens*, the "king of the dancing crane-flies." Mating takes place during the swarming, and the united pair generally leaves the main body of the swarm and flies away to a resting place.

The tipuline forms and some of the Limnobiinae (several species of Dicranomyia, species of Hexatoma, *Tipula macrolabis, T. fragilis, T. fuliginosa, T. taughannock*, and others) seem to mate without the preparatory operation of swarming, the males searching diligently and unceasingly for their mates, walking and fluttering about until they encounter the hiding female and then engaging in copulation. As stated by Needham (1908:215) in the case of *Dicranomyia simulans*, the males of this species seem to be very short-sighted and apparently unable to see their mates even when very close to them; they seem to rely mainly on the tactile nature of their long, filiform feet, which, the instant they come in contact with any part of the female, apprise the male of its proximity.

In some groups (Discobola, Liogma, Cylindrotoma, *Tipula ultima*, and others) the males mate with the females while the latter are still callow and teneral, in some cases even waiting beside the pupal case for the female to emerge, when she is at once engaged in copulation. In most cases, however, the female is fully developed and mature before mating takes place. When in copula most species rest quietly on some support, but nearly all species are quite capable of flying while still mated if disturbed; in such cases the larger sex takes the initiative — the female in the Tipulinae, the male in *Eriocera longicornis* and Teucholabis. Cases of mating between different species are rare, but in one instance the writer has noted the copulation of *Phalacrocera tipulina* with *Liogma nodicornis*.

Oviposition

The method of oviposition varies with the species and according to the structure of the ovipositor. In the forms with aquatic larvae (Eriocera, Hexatoma, and others) the eggs are laid directly in the water, the fly dipping during its flight. Many Tipula, such as *T. iroquois*, *T. bella*, and others, deposit their eggs regularly and methodically in algal beds at the edge of a stream. *Tipula nobilis*, one of the species having soft, blunt valves in the ovipositor, lays its eggs in soft mud or in moss. Many species of Limnophila deposit their eggs with great precision. The author has observed females of *Limnophila alleni* flying about low over the earth in cold, dark woods. They flutter along slowly and silently until a suitable place for egg-laying is found, consisting of a moss-covered, rotten log and the mud beneath it. The eggs are pushed firmly into their position by the acicular tergal valves of the ovipositor, considerable effort being made to place them securely. The rate of oviposition is not more than eight or ten eggs a minute, the female often pausing to rest for several seconds during the operation. When engaged in oviposition the fly is quite unconcerned with other agencies and may be picked up by hand.

The species of Tipula with a serrated ovipositor, as described on page 875, undoubtedly have a specialized method of egg-laying, tho what this may be is not yet known.

Photophilism

Many species of crane-flies, in widely separated groups, are attracted to light, such species being termed *photophilous*, or light-loving. It is

probable that this characteristic is fairly general among crane-flies. An interesting fact is that the great majority of specimens of photophilous species taken are either females, or males and females still in copulation, indicating a nocturnal or a crepuscular oviposition or mating habit for these species. There are many of these species, among them being *Erioptera septemtrionis, Limnophila adusta, Pedicia contermina, Nephrotoma ferruginea, Tipula apicalis, T. trivittata,* and *T. collaris.* It is these photophilous species that are so commonly found in houses, they being for the most part species that came to the lights at some earlier time.

ENEMIES

At all stages of their existence crane-flies are beset by enemies. The larvae and adults are preyed upon by a great variety of insect-eating birds and amphibia, and by many predacious insects such as beetles, asilid and empidid flies, Odonata, and the like. The larvae are parasitized by certain tachinid flies (Siphona, Admontia), and many internal parasites (Gregarinidae, Bacteria) and fungous diseases (Entomophthora [Empusa]) often prove fatal to crane-flies in their early stages. It is at their periods of transformation and while still soft and teneral that they are most susceptible to attack and injury of all kinds. The adult flies often serve as carriers of little red mites of the genera Trombidium and Rhyncholophus. This condition is very general and a great range of species are affected.

Many species of the family (Geranomyia, Dicranomyia, Limnophila, and others) live on the faces of vertical cliffs which are often wet with percolating and dropping water, and this results in a certain mortality due to the insects' being struck by the falling drops and dashed into the mud. During heavy rainfalls the smaller crane-flies rest on the underside of the leaves of trees, while the larger forms escape injury by hiding in crevices of the rock or the bark or by remaining closely pressed against the trunks of trees.

KEYS TO THE CRANE-FLIES OF NORTHEASTERN NORTH AMERICA

The species of crane-flies found in northeastern North America are included in four families, which may be separated according to the following key:

1. Five branches of the radius reaching the wing margin; a single anal vein . . . TANYDERIDAE (p. 883)
   Less than five branches of the radius reaching the wing margin; one or two anal veins . . . 2
2. Ocelli present . . . RHYPHIDAE (p. 886)
   Ocelli lacking . . . 3
3. A single anal vein . . . PTYCHOPTERIDAE (p. 884)
   Two anal veins (both running to the wing margin in all North American species; in some Old World forms the first anal vein fused with the second cubitus for a distance backward from the tip) . . . TIPULIDAE (p. 889)

FAMILY **Tanyderidae**

The remarkable primitive family Tanyderidae includes but two living genera — Tanyderus, of the antipodal regions, and Protoplasa, of the United States.

Genus **Protoplasa** Osten Sacken

1859 *Protoplasa* O. S. Proc. Acad. Nat. Sci. Phila., p. 252.

There are but two species of Protoplasa. The eastern species, *P. fitchii*, is discussed below. The western species, *P. vipio*, ranges from Colorado to California.

Protoplasa fitchii O. S.

1859 *Protoplasa fitchii* O. S. Proc. Acad. Nat. Sci. Phila., p. 252.

The species *Protoplasa fitchii* is of medium size and bears a curious superficial resemblance to the common tipulid *Epiphragma fascipennis*. It is a very rare insect, there being scarcely a score of specimens in the various collections, most of them from the Adirondacks of New York State and the Black Mountains of North Carolina. The fly is brownish gray, the wings being marked with an ocellate pattern of spots and bands (Plate XXX, 1). The anal angle of the wing, which is almost square, is very prominent. The immature stages are unknown but the writer surmises that they occur in wet wood in the same situations as the larvae and pupae in the genus Epiphragma.

FAMILY **Ptychopteridae**

The family Ptychopteridae has generally been understood to include the tanyderid flies, as well as the three genera herein considered as constituting it. The resemblance between the Tanyderidae and the Ptychopteridae seems to be superficial only, however, and the differences are very considerable.

The immature stages of the Ptychopteridae are very remarkable. The larva lives in an aquatic or a semi-aquatic habitat, and its caudal extremity is provided with an extensile elongated breathing tube which bears the spiracles at the end. The pupa has one of the two thoracic breathing horns enormously elongated, while the other is considerably atrophied. Both these elongated processes in the immature stages serve to provide the insect with air while the body is submerged beneath the mud and water. The larvae of Bittacomorpha are of a peculiar rust-red color; those of Bittacomorphella are almost black, with the short breathing horns yellow; those of Ptychoptera are more yellowish brown.

The following key divides the family into its genera:

1. Antennae 20-segmented; wings with cell M_2 lacking; legs banded with black and white. (Subfamily **Bittacomorphinae.**)..2
   Antennae 16-segmented; wings with cell M_2 present; legs not banded with black and white. (Subfamily **Ptychopterinae.**)....................*Ptychoptera* Meig. (p. 884)
2. Apex of the wing not pubescent; metatarsi swollen.......*Bittacomorpha* Westw. (p. 884)
   Apex of the wing pubescent; metatarsi not swollen.......*Bittacomorphella* Alex. (p. 885)

SUBFAMILY **Ptychopterinae**

Genus **Ptychoptera** Meigen

1803 *Ptychoptera* Meig. Illiger's Mag., vol. 2, p. 262.

Ptychoptera rufocincta O. S.

1859 *Ptychoptera rufocincta* O. S. Proc. Acad. Nat. Sci. Phila., p. 252.

Ptychoptera rufocincta is the only eastern species of Ptychoptera. It is deep black, with rusty-red bands on the abdominal segments; the wings (Plate XXX, 2) have brown crossbands, presenting an appearance superficially very like that of *Limnophila macrocera.*

SUBFAMILY **Bittacomorphinae**

Genus **Bittacomorpha** Westwood

1835 *Bittacomorpha* Westw. London and Edinburgh Phil. Mag., vol. 6, p. 281.

There are two described species of Bittacomorpha inhabiting the Nearctic region, one, *Bittacomorpha clavipes* (Fabr.), in the East, and one, *B. occidentalis* Ald., in the West. *B. clavipes* has been reported from Brazil but the record needs confirmation.

Bittacomorpha, or the "phantom crane-fly," is among the most interesting of the local genera. The larger and commoner eastern species, *B. clavipes*, is one of the most abundant and widely distributed of the North American crane-flies, and inhabits wet swales, swamps, margins of ponds, and similar situations. The legs are curiously banded with black and white. The thoracic dorsum is deep velvety black with a white median line. The swollen metatarsi are unique among the local crane-flies. The wing is shown in Plate XXX, 3. The larva of this species is very similar in structure to that of species of Ptychoptera, but is easily distinguished by the rust-red tomentum which completely covers the body. Both these genera have the extensile breathing tube in the larva, and the single enormously produced breathing spiracle in the pupa. The larvae are common in rotting organic vegetable matter which is percolated and saturated with running water. The adult flies are very conspicuous and attract considerable attention even among persons who are not greatly interested in insects. The long, swollen legs, radiating out from the body like the spokes from the hub of a wheel and conspicuously banded with black and white, make the flies noticeable as they drift slowly thru the air, apparently as light as bits of down.

Genus **Bittacomorphella** Alexander

1916 *Bittacomorphella* Alex. Proc. Acad. Nat. Sci. Phila., p. 545.

The genus Bittacomorphella includes two known species, both of the Nearctic region. Of these, *Bittacomorphella jonesi* (Johns.) is eastern, and the larger species, *B. sackenii* (Röder), is western. The better-known of the two species, *B. jonesi*, is locally common in cold, shaded situations, as along dark ravines, near running water, or beneath dark bridges and culverts. The curious black larva is found in mud or moist earth, in haunts similar to those described for the adult. The flies are readily distinguished from those of the larger and somewhat similar *Bittacomorpha clavipes* by the metatarsi, which are not swollen and have no white near the base but are marked with more or less white at the tips, these white markings being broadest on the fore legs and narrowest on the hind legs.

The tibiae are black, with a broad white band beyond the base. The second and third tarsal segments are pure white. The apically pubescent wings (Plate XXX, 4) are characteristic of the genus.

FAMILY Rhyphidae

The family Rhyphidae includes an apparently heterogeneous group of three subfamilies which, until a very recent date, were placed in three widely separated families of the nematocerous Diptera. The Rhyphidae comprise about fifty species, arranged in some seven genera. The family has long been held to contain only the genus Rhyphus and one or two closely allied exotic genera. In 1916, Edwards (1916) removed the genus Mycetobia from the family Mycetophilidae and placed it with the Rhyphidae. A critical study of the immature stages of the genus Trichocera now demonstrates that this group, likewise, should be placed in very close proximity to the Rhyphinae. In general appearance the three groups or subfamilies herein considered as comprising the Rhyphidae differ greatly, but the larvae of all members are so unmistakably related that there can be no question of the close phylogenetic relationship.

The Trichocerinae have the more generalized wing venation, there being three branches to the sector and three to the media, and two distinct anal veins. The local species of Trichocera have the *m-cu* cross-vein punctiform or obliterated by a slight fusion of Cu_1 on M_3. *Trichocera trichoptera* O. S., of the Western States, has the cross-vein very long and conspicuous. The second anal vein is long and subsinuate in the subgenus Diazosma Bergr., but very short and recurved in the typical subgenus, in *T. trichoptera* being very short and reduced and narrowing the second anal cell.

Edwards (1916) and Knab (1916) have recently shown the probable evolution of Mycetobia from the more generalized Rhyphidae such as Rhyphus and Olbiogaster. The most important venational feature to be considered is the reduction of the media in the Mycetobiinae, but two branches persisting in Mycetobia and the vein tending to be evanescent in the Ethiopian genus Mesochria. Species of Olbiogaster in some cases have the posterior branch of the media less strongly chitinized than the anterior fork, and probably indicate the manner in which the vein is reduced. An entirely comparable case is seen in the related family Ptychopteridae (comparing Ptychoptera and Bittacomorpha). In the

Rhyphidae, the Trichocerinae are the most generalized, the Mycetobiinae the most specialized, of the groups.

The subfamilies may be separated by the following key:

1. Two distinct anal veins; radial sector three-branched............ **Trichocerinae** (p. 887)
   A single distinct anal vein; radial sector two-branched.............................. 2
2. Cell *1st* M_2 present.. **Rhyphinae** (p. 888)
   Cell *1st* M_2 lacking.. **Mycetobiinae** (p. 888)

SUBFAMILY **Trichocerinae**

The subfamily Trichocerinae includes but two genera — Trichocera, and Ischnothrix Bigot of Cape Horn.

Genus **Trichocera** Meigen

1800 *Petaurista* Meig. Nouv. Class. Mouch., p. 15 (*nomen nudum*).
1803 *Trichocera* Meig. Illiger's Mag., vol. 2, p. 262.
1911 *Paracladura* Brun. Rec. Indian Mus., vol. 6, p. 286.

In the genus Trichocera there are about twenty described species, of which the majority are Holarctic in their distribution but a few are from India and the antipodes. The species of this genus are in a very chaotic condition taxonomically, and it seems difficult to remedy this until the European and American forms can be critically studied and compared. There can be little doubt that many of the species are Holarctic in their distribution and the three or four evident species within the limits here considered may be conspecific with the European forms. The larvae, so far as known, live in decaying vegetable matter (Johannsen, 1910). The adult flies are common in autumn and early spring, and appear in small swarms on warm, sunny days in winter. During the winter months they are often found in cellars, resting on the windows. They are also to be found in mines, and the writer has seen specimens from a Colorado silver mine taken at a very considerable depth by Dr. H. B. Hungerford. Some of the swarms of these flies number many thousands of individuals.

The following key divides the local species of Trichocera:

1. Second anal vein subsinuate; veins long-hairy; ovipositor fleshy. (Subgenus *Diazosma* Bergr.) [Journ. N. Y. Ent. Soc., vol. 24, p. 124–125, pl. 8, fig. 10. 1916.] (Plate XLI, 166.)........................ *T. subsinuata* Alex.
   Second anal vein short, incurved to the anal angle; veins not long-hairy; ovipositor chitinized, turned downward, the concavity being on the lower face. (Subgenus *Trichocera* Meig.)........................ 2
2. Wings with two brown clouds. [List Dipt. Brit. Mus., vol. 1, p. 84. 1848.] *T. bimacula* Walk.
   Wings unicolorous. [Winter Insects of New York, p. 9. 1848.] (Plate XLI, 165.) *T. brumalis* Fitch

Certain European species of Trichocera, such as *T. maculipennis* (Fabr.) and *T. regelationis* (Linn.), have been recorded from the Northern States and Canada; these records may be correct, since, as stated above, it is very probable that many species of the genus are Holarctic in their distribution. If such is the case, the names used in the preceding key are very probably synonyms of the European species.

SUBFAMILY **Rhyphinae**

The subfamily Rhyphinae includes but three genera. The two which are represented by North American species are Rhyphus, with about a score of principally Holarctic species, and Olbiogaster, a tropical group of five species. Within the limits of this paper three species occur, two of which — *Rhyphus fenestralis* and *R. punctatus* — are very widespread over the North Temperate Zone.

Genus **Rhyphus** Latreille

1805 *Rhyphus* Latr. Hist. Nat. Crust. et Ins., vol. 14, p. 291.

The adult flies of the genus Rhyphus are often found resting on the trunks of trees or on near-by vegetation. The immature stages are spent in decaying vegetable matter, manure, sewage, and similar situations. The venation of a typical Rhyphus is shown in figure 132, A.

Baerg (1918) has recently published a key for the separation of the adult flies of the three eastern-North-American species of the genus. This key is here modified to conform with the other keys in this paper:

1. Basal deflection of M_2 as long as, or longer than, m (that is, veins M_1, M_2, and M_3 about equidistant from one another at cell *1st* M_2) 2
   Basal deflection of M_2 much shorter than m; eyes of male holoptic; no yellowish spot near midlength of costal margin of wing . . . . *R. punctatus* (Fabr.)
2. Wing with a distinct yellowish spot near midlength of costal margin; subapical hyaline spots sharply defined; eyes of male holoptic; median prescutal stripe split by a narrow gray line, more distinct in the female . . . . *R. alternatus* Say
   Wing with the yellow and hyaline spots less distinct and more diffuse; eyes of both sexes dichoptic; median prescutal stripe only indistinctly divided, if at all. *R. fenestralis* (Scop.)

SUBFAMILY **Mycetobiinae**

The subfamily Mycetobiinae, so far as known, includes only the genus Mycetobia, discussed below, and the genus Mesochria of the Seychelles Islands. Other genera have been associated with Mycetobia in the Mycetophilidae, but so far as is known their larvae are quite normal for

the latter family and quite unlike the amphipneustic larvae of the Rhyphidae. Until additional data are forthcoming they should be considered as being Mycetophilidae.

Genus **Mycetobia** Meigen

1818 *Mycetobia* Meig. Syst. Beschr., vol. 1, p. 229.

Johannsen (1909) recognizes six recent species of Mycetobia, and five others as fossil in Baltic amber (Eocene). The larvae are found in decaying

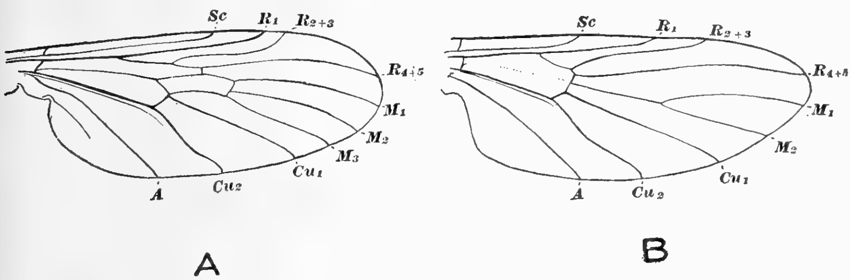


FIG. 132. WING VENATION IN RHYPHIDAE

A, Venation of typical Rhyphus. B, Venation of Mycetobia

trees and in fermented sap in the wounds of trees. A single species is known from New York State, *Mycetobia divergens* Walk. The characteristic venation of the genus is shown in figure 132, B.

FAMILY **Tipulidae**

The family Tipulidae includes almost all of the local crane-flies. It is divided into three subfamilies, two of which are further separable into nine tribes — six belonging to the Limnobiinae and three to the Tipulinae. The tribes may be separated as follows:

1. Last segment of the palpi elongate, whiplash-like; nasus usually distinct; antennae usually with 13 segments; *Sc* almost always ending in *R*; *m-cu* cross-vein present or obliterated by the usually slight fusion of Cu_1 on M_{3+4}. In the dolichopezine genus Brachypremna (p. 928) *Sc* is very long and ends in the costa, and the fusion of Cu_1 and M_{3+4} is often extensive; but the antennae are 13-segmented, the palpi are elongated, the nasus is distinct, and the whole appearance of the fly is decidedly tipuline. (Subfamily **Tipulinae**.) 2

   Last segment of the palpi short; no distinct nasus; antennae usually 14- or 16-segmented; *Sc* usually ending in costa but connected with *R* by Sc_2; *m-cu* cross-vein obliterated by the long fusion of Cu_1 on M_{3+4}. In Pedicia (p. 923) the palpi are elongated, but all other characters are limnobiine. (Subfamilies **Limnobiinae**, **Cylindrotominae**.) 4

2. Vein R_2 obliterated by atrophy (this is also the case to a lesser extent in *Tipula subfasciata* and *T. penobscot*), or else (as in Brachypremna) the second anal vein very short, not more than one-third the length of the first anal vein; legs very slender, filiform .... *Dolichopezini* (p. 928)
   Vein R_2 present for its entire length (except in *Tipula subfasciata*, *T. penobscot*, and other species); second anal vein longer, one-half the length of first anal vein; legs stouter and usually shorter than in Dolichopezini 3
3. Antennae without verticils (see Stygeropis, below); flagella of the male antennae pectinate .... *Ctenophorini* (p. 930)
   Antennae verticillate (except in Stygeropis and most species of Holorusia); flagella of the male antennae not pectinate (in some species of Nephrotoma and Tipula the ventral face of the segments is often deeply incised, producing a serrate appearance, but the antennae in the northern forms are never pectinate) .... *Tipulini* (p. 932)
4. Four branches of radius reaching the margin (see note on *Gonomyia blanda*, below) 5
   Two or three branches of radius reaching the margin 9
5. Tibiae spurred at tip 6
   Tibiae without spurs at tip. (*Gonomyia blanda*, p. 905, has R_2 in close proximity to R_1 at the wing margin, so that but three branches of the radius appear to reach the wing margin; the tropical antochine genus Paratropeza will also run to here, and has been mistaken by some authors for a Gnophomyia; the investigator must always be on the lookout for such aberrant genera and species, especially when dealing with tropical material.) .... *Eriopterini* (p. 901)
6. Antennae with from 6 to 10 segments .... *Hexatomini* (p. 920)
   Antennae with more than 10 segments 7
7. Sc_2 beyond the origin of Rs .... *Limnophilini* (p. 913) (except genus Ula)
   Sc_2 before the origin of Rs 8
8. Antennae 17-segmented; wings pubescent .... Genus *Ula*, tribe *Limnophilini* (p. 913)
   Antennae 13- to 16-segmented; wings glabrous .... *Pediciini* (p. 923)
9. Tibiae spurred; an apparent fusion of R_{1+2+3} to the wing margin so that but two branches of the radius are present (except in *Phalacrocera neoxena*, in which three branches are present). The European hexatomine genus Cladolipes runs to here but has only eight antennal segments; the South American species *Psaronius abnormis* also comes here, but may be readily separated by the very elongate subcosta.
   Subfamily **Cylindrotominae** (p. 926)
   Tibiae without spurs; no contiguity of R_1 and R_{2+3} at their tips 10
10. Antennae 12-, 15-, or 16-segmented; claws usually without teeth on their lower side .. 11
    Antennae 14-segmented; claws with teeth on their lower side .... *Limnobiini* (p. 890)
11. Cross-vein r lacking; Sc ending before the origin of the short Rs; R_{2+3} upcurved at the end, R_{4+5} bent strongly toward the apex of the wing producing a trumpet-shaped cell R_3; cell *1st* M_2, when present, pointed at the inner end.
    Subgenus *Leiponeura*, genus *Gonomyia*, tribe *Eriopterini* (p. 905)
    Cross-vein r present or lacking; if lacking, Sc ends far beyond the origin of Rs; R_{2+3} not strongly upcurved at end, and R_{4+5} not bent strongly toward the apex of the wing; inner end of cell *1st* M_2 not pointed .... *Antochini* (p. 897)

The nearly wingless snow fly, Chionea, belongs to the tribe Eriopterini (page 902).

SUBFAMILY **Limnobiinae**

Tribe **Limnobiini**

The genera of the tribe Limnobiini may be separated by the following key:

1. Rostrum elongated, longer than head and thorax together ...... *Geranomyia* Hal. (p. 891)
   Rostrum not elongated, shorter than the head 2

2. A supernumerary cross-vein in cell *1st A*, connecting the two anal veins. *Discobola* O. S. (p. 892)
   No supernumerary cross-vein in cell *1st A*....................................3
3. Often with a supernumerary cross-vein in cell *Sc*; antennae of the male bi-, uni-, or sub-pectinated....................*Rhipidia* Meig. (p. 892)
   No supernumerary cross-vein in cell *Sc* (excepting a weak one in *Dicranomyia simulans*); antennae of the male not pectinated....................................4
4. *Sc* usually short, ending opposite the origin of *Rs*; claws usually with but a single tooth on the lower side; ventral pleural appendage of the male hypopygium a fleshy lobe. *Dicranomyia* Steph. (p. 893)
   Sc always elongate, ending far beyond the origin of *Rs*; *r* often considerably removed from the tip of R_1; claws usually with two or three teeth on the lower side; ventral pleural appendage of the male hypopygium horny...........*Limnobia* Meig. (p. 895)

Genus **Geranomyia** Haliday

1833 *Geranomyia* Hal. Ent. Mag., vol. 1, p. 154.
1835 *Limnobiorhynchus* Westw. Ann. Soc. Ent. France, vol. 4, p. 683.
1838 *Aporosa* Macq. Dipt. Exot., vol. 1, p. 62.
1865 *Plettusa* Phil. Verh. Zool.-Bot. Ges. Wien, p. 597.

The genus Geranomyia includes about seventy described forms, the species being most numerous in the Neotropical and Oriental regions. The species are readily distinguished from all other crane-flies by the curious elongate rostrum (fig. 124, A, page 846). The four species occurring within the limits considered in this paper are common and widely distributed; further notes on their distribution have been given by the writer in an earlier paper on the genus (Alexander, 1916:486–496). Nothing is known concerning their immature stages, this being one of the most conspicuous gaps in the whole family. It is probable that *G. rostrata*, at least, is partly aquatic, living in moist earth or possibly in wet moss.

The following key divides the local species of the genus:

1. Wings heavily spotted with dark brown; tips of the tibiae black. [*Limnobia rostrata* Say. Journ. Acad. Nat. Sci. Phil., vol. 3, p. 22. 1823.] (Plate XXXI, 10.)..*G. rostrata* (Say)
   Wings unmarked or with only pale indistinct seams along the cord..................2
2. *Sc* short, ending opposite or just beyond the origin of *Rs*; cross-veins and deflections of veins faintly seamed with darker. [Proc. Acad. Nat. Sci. Phil., p. 207. 1859.] (Plate XXXI, 13.)..*G. diversa* O. S.
   Sc long, ending at about midlength of the sector; wings unmarked except for the stigmal spot..3
3. Body coloration yellow; wings with the stigma pale; legs dull yellow, the femora not darkened at their tips. [Journ. N. Y. Ent. Soc., vol. 8, p. 186, pl. 7, fig. 13. 1900.] (Plate XXXI, 12.)..*G. distincta* Doane
   Body coloration yellowish brown, darkest on the scutal lobes and the postnotum; wings with the stigma oval, dark brown, well-defined; legs brownish yellow, the femora brown at the tips. [*Limnobiorhynchus canadensis* Westw. Ann. Soc. Ent. France, vol. 4, p. 684. 1835.] (Plate XXXI, 11.)........................*G. canadensis* (Westw.)

G. canadensis is most commonly found along small streams near cliffs; *G. diversa*, resting on vegetation along running water or clinging to vertical wet banks; *G. rostrata*, on rich vegetation in damp places, where it is often extremely abundant (Alexander, 1912:67–68). The habits of the adult flies are discussed on page 878.

Genus **Discobola** Osten Sacken

1865 *Discobola* O. S. Proc. Ent. Soc. Phil., p. 226.
1869 *Trochobola* O. S. Mon. Dipt. N. Amer., part 4, p. 98.

The genus Discobola is a well-defined group including eight described species with a curious discontinuous distribution — two species occurring in North America, two in Europe, and four in New Zealand. The species are readily distinguished by the presence of a strong supernumerary cross-vein between the two anal veins. The only local species is *D. argus*.

Discobola argus (Say)

1824 *Limnobia argus* Say. Long's Exped., App., p. 358.
1865 *Discobola argus* O. S. Proc. Ent. Soc. Phil., p. 226.

The species *Discobola argus* is a curious fly, with ocellate markings on the yellowish white wings (Plate XXXII, 41). The body coloration is yellowish, the thorax with three brown stripes, each femur with a brown subterminal ring. The immature stages of the American species are unknown but are probably spent in decaying pine stumps, as are those of the European *D. caesarea*; specimens of *D. argus* have been observed mating on the bark of stumps (in Ithaca, New York, October 3, 1912, by Ilg and Alexander). The fly is uncommon in May and June but becomes more numerous from August to October.

Genus **Rhipidia** Meigen

1818 *Rhipidia* Meig. Syst. Beschr., vol. 1, p. 153.

In the genus Rhipidia there are about twenty-eight described species, most numerous in the tropics of the New World. The character of the pectination of the antennae (page 851) varies in the different groups or subgenera as follows:

Rhipidia Meig. (*maculata*, *bryanti*) — antennae of the male bipectinate.
Monorhipidia Alex. (*fidelis*) — antennae of the male unipectinate.
Arhipidia Alex. (*domestica*, *shannoni*) — antennae of both sexes subpectinate to simple.

The immature stages of the known species are spent in decaying vegetable matter, manure, or decaying fungi (*R. maculata*, *R. domestica*), in decaying wood or beneath the loose bark of trees (*R. uniseriata*, *R. fidelis*, *R. bryanti*), or perhaps in aquatic situations (*R. maculata*, according to Needham).

The following key divides the local species of the genus:

1. Wings with an abundant pale brown or gray dotting in all the cells..................2
   Wings with the markings larger and confined to the vicinity of the veins.............3
2. Body coloration grayish, the prescutum with a broad black median line; postnotum gray; wings with a heavy brown pattern along the costal margin, the marks about equal to the interspaces; legs brown; male antennae bipectinate. [Syst. Beschr., vol. 1, p. 153, pl. 5, fig. 11. 1818.] (Plate XXXII, 36.)..........*R. maculata* Meig.
   Body coloration yellowish brown, the prescutum without a broad black median line; postnotum black; wings with small black spots at the base, the subcostal cross-vein, the origin of the sector, and the stigma, these marks much smaller than the interspaces; legs yellow; male antennae subpectinate. [Proc. Acad. Nat. Sci. Phila., p. 581, pl. 27, fig. 23. 1914.] (Plate XXXII, 39.)............................*R. shannoni* Alex.
3. Prescutum reddish brown with narrow black lines; pleura dull yellow with two narrow blackish longitudinal stripes; antennae with segments 12 and 13 light yellowish; basal deflection of Cu_1 usually far before the fork of M; antennae of the male subpectinate. [Proc. Acad. Nat. Sci. Phila., p. 208, pl. 3, figs. 8, 9. 1859.] (Plate XXXII, 40.) *R. domestica* O. S.
   Prescutum gray with a broad black median line; pleura grayish or plumbeous, unstriped; antennae black thruout; basal deflection of Cu_1 at the fork of M; antennae of the male not subpectinate...4
4. Wings with the dark pattern beyond the origin of the sector only, a large rounded cloud at the origin and fork of the sector, the large rectangular stigma and the radial cells largely darkened; abdomen dark brown, the genitalia reddish yellow; antennae of the male unipectinate. [Proc. Acad. Nat. Sci. Phila., p. 209. 1859.] (Plate XXXII, 38.)..*R. fidelis* O. S.
   Wings with a series of about five large grayish brown blotches along the costal margin, two before the origin of the sector; abdominal tergites yellow, the caudal half of each segment dark brown; antennae of the male bipectinate. [Proc. Boston Soc. Nat. Hist., vol. 34, p. 123, 124, pl. 16, fig. 20. 1909.] (Plate XXXII, 37.)..*R. bryanti* Johns.

R. domestica and *R. shannoni* are more southern in their distribution, *R. fidelis* and *R. maculata* more northern. Some of the species have a very extensive geographical range, *R. domestica* and its races occurring from Alaska to Argentina, and *R. maculata* being found thruout northern Europe and North America.

Genus **Dicranomyia** Stephens

1829 *Dicranomyia* Steph. Cat. Brit. Ins., vol. 2, p. 243.
1830 *Siagona* Meig. Syst. Beschr., vol. 6, plate 65, fig. 7.
1854 *Numantia* Bigot. Ann. Soc. Ent. France, ser. 3, vol. 2, p. 470.

Dicranomyia is one of the largest of the crane-fly genera, there being from one hundred and eighty to one hundred and ninety described species,

found on all the continents and on many of the oceanic islands. The species are rather small, are dull-colored, and are often difficult of exact determination.

The immature stages are spent in a wide range of habitats, described on page 838

The local species of the genus Dicranomyia may be separated according to the following key:

1. Wings with but one free branch of the media reaching the margin. [23d Rept. N. Y. State Ent., p. 211–212, pl. 27, fig. 5. 1908.] (Plate XXXI, 15.). . *D. whartoni* Needm.
   Wings with two free branches of the media reaching the margin. .2
2. Wings narrow, lanceolate; cell *1st* M_2 open; thoracic pleura with a brown longitudinal stripe. [*Limnobia longipennis* Schum. Beitr. zur Ent., vol. 1, p. 104, pl. 1, fig. 2. 1829.] (Plate XXXI, 14.) . . . . *D. longipennis* (Schum.)
   Wings broad. 3
3. *Sc* ending opposite, or before or slightly beyond the origin of the sector. 4
   Sc ending far beyond the origin of the sector. 20
4. Antennae with at least the basal segments pale. 5
   Antennae with the segments dark thruout. 9
5. Cell *1st* M_2 open (cross-vein *m* lacking) 6
   Cell *1st* M_2 closed. 7
6. Prescutum with a single brown stripe; dorsal pleural appendage of the male hypopygium a short hook. [Proc. Acad. Nat. Sci. Phila., p. 211. 1859.] . . . . . . *D. immodesta* O. S.
   Prescutum with three brown stripes; dorsal pleural appendage of the male hypopygium a long, saber-like hook, which is contiguous with its mate on the opposite side. [Proc. Acad. Nat. Sci. Phila., p. 212, pl. 3, fig. 5. 1859.] . . . . *D. gladiator* O. S.
7. Pale yellowish thruout, only the tips of the tarsi and the eyes darker; in life the abdominal segments somewhat greenish. [Proc. Acad. Nat. Sci. Phila., p. 212. 1859.] (Plate XXXI, 22.) . . . . *D. pudica* O. S.
   Brownish yellow, the antennae darkened at the tips; halteres brownish. 8
8. Halteres pale, the knobs infuscated; abdomen brownish yellow. [Journ. N. Y. Ent. Soc., vol. 8, p. 183, pl. 7, fig. 5. 1900.] . . . . *D. isabellina* Doane
   Halteres and abdomen brown. [Proc. Acad. Nat. Sci. Phila., p. 212. 1859.] *D. diversa* O. S.
9. Cell *1st* M_2 open; *Sc* far before the origin of *Rs*, due to the shortness of the latter which is about equal to the basal deflection of R_{4+5}. 10
   Cell *1st* M_2 closed; *Sc* nearly opposite the origin of *Rs*, which is much longer than the basal deflection of R_{4+5}. 11
10. Rostrum elongated, nearly as long as the head, brown; prescutum with a single dark brown stripe. [Mon. Dipt. N. Amer., part 4, p. 65. 1869.] (Plate XXXI, 16.) *D. rostrifera* O. S.
    Rostrum much shorter than the head, light yellow; prescutum with three dark brown stripes. [Mon. Dipt. N. Amer., part 4, p. 66. 1869.] . . . . *D. brevivena* O. S.
11. Thorax shining black, the pleura with a grayish pruinosity. [Proc. Acad. Nat. Sci. Phila., p. 17. 1860.] (Plate XXXI, 23.) . . . . *D. morioides* O. S.
    Thorax not shining black; gray, brown, or yellowish brown. 12
12. Femora brown with the tips broadly yellow; wings marked with brown. [*Limnobia badia* Walker. List Dipt. Brit. Mus., vol. 1, p. 46. 1848.] (Plate XXXI, 20.) *D. badia* (Walk.)
    Femora not banded with yellow; wings unmarked or nearly so. 13
13. Sc_1 much longer than Sc_2, being nearly if not quite the length of the stigma. 14
    Sc_1 short, not more than one-half the length of the stigma. 16

14. Halteres elongated (northern species). [Mon. Dipt. N. Amer., part 4, p. 71. 1869.] (Plate XXXI, 18.) .... *D. halterata* O. S.
Halteres short, of normal length 15
15. Prescutum reddish brown, with a narrow paler median line. [Journ. N. Y. Ent. Soc., vol. 8, p. 184, pl. 7, fig. 6. 1900.] .... *D. brunnea* Doane
Prescutum dark brown with yellow and brown stripes. [Proc. Acad. Nat. Sci. Phila., p. 211. 1859.] .... *D. distans* O. S.
16. Coloration gray, the prescutum with a broad median brown stripe; a narrow brown seam on cross-vein *r*. [Proc. Acad. Nat. Sci. Phila., p. 209, pl. 3, figs. 4, 4a. 1859.] (Plate XXXI, 21.) .... *D. liberta* O. S.
Coloration brown or yellowish brown; no narrow brown seam on cross-vein *r* 17
17. Basal deflection of M_{1+2}, forming the inner end of cell *1st* M_2, arcuated so that cells *1st* M_2 and R_3 are almost on a line. [Proc. Acad. Nat. Sci. Phila., p. 210. 1859.] .... *D. stulta* O. S.
Basal deflection of M_{1+2} not conspicuously arcuated, cell *1st* M_2 being conspicuously more distant from the wing base than cell R_3 18
18. Thorax brown, with three blackish stripes on the prescutum which are confluent, the lateral ones running caudad onto the scutal lobes; wings hyaline, unmarked. [*Furcomyia monticola* Alex. Psyche, vol. 18, p. 201–202, pl. 16, fig. 7. 1911.] (Plate XXXI, 19.) .... *D. monticola* (Alex.)
(*Dicranomyia monticola* may not be distinct from *D. stulta*, which appears to be a somewhat variable species.)
Thorax not so marked; wings with a grayish or brownish tinge 19
19. Thorax brownish yellow, with a darker brown median stripe; antennae black. [Mon. Dipt. N. Amer., part 4, p. 70–71, pl. 1, fig. 3. 1869.] (Plate XXXI, 17.) *D. haeretica* O. S.
Thorax light brown without a distinct darker median stripe; antennae reddish brown. [Journ. N. Y. Ent. Soc., vol. 8, p. 184, pl. 7, fig. 8. 1900.] .... *D. moniliformis* Doane
20. Wings spotted with darker 21
Wings unmarked, except for the stigmal spot when it occurs 22
21. Wings with brown dots in all the cells; femora with a yellowish ring before the tip. [*Limnobia simulans* Walk. List Dipt. Brit. Mus., vol. 1, p. 45. 1848.] (Plate XXXI, 24.) .... *D. simulans* (Walk.)
Wings with three large brown spots along the costa, the first at the origin of the sector, the second at the tip of *Sc*, and the third at the tip of R_1; wings grayish brown, paler near the stigma; cord and outer end of cell *1st* M_2 seamed with dark brown; femora without a yellowish ring before the tip. [Mon. Dipt. N. Amer., part 4, p. 75. 1869.] (Plate XXXI, 25.) .... *D. rara* O. S.
22. Wings with a distinct pubescence in the apical cells. [Proc. Acad. Nat. Sci. Phila., p. 211. 1859.] (Plate XXXI, 28.) .... *D. pubipennis* O. S.
Wings glabrous on all the cells 23
23. No stigmal spot nor brown seams to the veins; R_1 strongly curved toward R_{2+3} at the tip; tarsi brown. [Mon. Dipt. N. Amer., part 4, p. 74. 1869.] (Plate XXXI, 27.) *D. globithorax* O. S.
Stigma evident, dark brown; paler brown seams to the cord and the outer end of cell *1st* M_2; R_1 not incurved toward R_{2+3}; tarsi whitish. [Can. Ent., vol. 48, p. 42–43. 1916.] (Plate XXXI, 26.) .... *D. macateei* Alex.

Genus **Limnobia** Meigen

1800 *Amphinome* Meig. Nouv. Class. Mouch., p. 15 (*nomen nudum*).
1803 *Limonia* Meig. Illiger's Mag., vol. 2, p. 262.
1818 *Limnobia* Meig. Syst. Beschr., vol. 1, p. 116.
1856 *Limnomyza* Rond. Prodromus, vol. 1, p. 185.

Limnobia is a rather small genus of usually handsome flies, including about thirty-five described species. The species are most numerous in Europe and North America, but a very few range into the tropics of both hemispheres. Most of the crane-flies described as species of Limnobia before the partition of the genus, do not belong here at all.

The haunts of the immature stages, so far as known, include a considerable range of habitats, from possibly aquatic forms (*L. parietina*) to those living in moist earth near streams (*L. fallax* and probably *L. solitaria*), in decaying vegetable matter (*L. indigena*, according to Greene), in decaying leaves (*L. nigropunctata*, *L. flavipes*, *L. tripunctata*), in rotten wood (*L. cinctipes*, *L. annulus*, *L. dumetorum*, and others), and in fungi (*L. triocellata*, *L. xanthoptera*, and often *L. cinctipes* and *L. annulus*).

The local species of Limnobia may be separated according to the following key:

1. Cross-vein *r* at the tip of R_1 2
   Cross-vein *r* removed from the tip of R_1 7
2. Knob of the halteres black 3
   Knob of the halteres pale at the apex 6
3. Femora yellow, the extreme tips narrowly dark brown; wings yellowish, with three eye-like markings. [Proc. Acad. Nat. Sci. Phila., p. 216. 1859.] (Plate XXXII, 34.) *L. triocellata* O. S.
   Femora with one or more dark brown rings before the dark tips; wings without an ocellate pattern 4
4. Wings with four large dark brown spots in cell *R* that are about equidistantly spaced. [Proc. Acad. Nat. Sci. Phila., p. 289. 1861.] .... *L. hudsonica* O. S.
   Wings not with four large brown equidistant spots in cell *R* 5
5. Small, wing of female about 9.5 mm.; wings narrow, with a distinct dark brown pattern; spots in cell *R* small, clear-cut, dark brown. [Proc. Boston Soc. Nat. Hist., vol. 34, p. 125. 1909.] (Plate XXXII, 32.) .... *L. fallax* Johns.
   Larger, wing of female about 11 mm.; wings broader, with the pattern paler brown, more diffused; spots in cell *R* larger, often poorly defined and sometimes confluent, medium brown. [Proc. Acad. Nat. Sci. Phila., p. 215, pl. 3, fig. 6. 1859.] (Plate XXXII, 31.) *L. solitaria* O. S.
6. Femora with three brown bands. [Proc. Acad. Nat. Sci. Phila., p. 214. 1859.] *L. immatura* O. S.
   Femora with two brown bands. [Journ. Acad. Nat. Sci. Phila., vol. 3, p. 21. 1823.] (Plate XXXII, 29.) .... *L. cinctipes* Say
7. Wings with brown clouds and seams 8
   Wings nearly clear, at most with three or four small brown dots along the costal margin 9
8. Large species, wing 15 mm.; wing apex very blunt; all the cells clouded and marbled medially with gray and brown. [Proc. Acad. Nat. Sci. Phila., p. 289. 1861.] (Plate XXXII, 30.) .... *L. parietina* O. S.
   Small species, wing under 12 mm.; wing apex normal; apical cell with the markings confined to the region near the veins. [Proc. Acad. Nat. Sci. Phila., p. 215, pl. 3, fig. 3. 1859.] (Plate XXXII, 33.) .... *L. indigena* O. S.

9. Wings with three small brown dots along the costal margin; head dark; antennae darkened toward the tips. [Proc. Acad. Nat. Sci. Phila., p. 216. 1859.] (Plate XXXII, 35.) *L. tristigma* O. S.
Wings yellowish, unspotted; head yellow, excepting the front; antennae yellow. [Mon. Dipt. N. Amer., part 4, p. 95. 1869.] .... *L. sociabilis* O. S.

Limnobia cinctipes runs very close to *L. immatura* and apparently cannot always be distinguished from it; the character of an ocellate, yellow, brown-encircled mark at the stigma in *L. cinctipes* and a solid brown one in *L. immatura* does not hold in a series. *L. hudsonica*, *L. solitaria*, and *L. fallax* represent another group of closely related species. *L. sociabilis* is very rare and its exact status is still not well understood.

Tribe **Antochini**

The genera of the tribe Antochini may be classified in accordance with the following key:

1. Rostrum elongated, at least as long as the head 2
Rostrum shorter than the head 4
2. Rostrum about as long as the head or a very little longer ..... *Rhamphidia* Meig. (p. 897)
Rostrum about as long as the body 3
3. *Rs* with two branches reaching the wing margin .... *Elephantomyia* O. S. (p. 898)
Rs with a single branch reaching the wing margin .... *Toxorhina* Loew (p. 898)
4. Cross-vein *r* lacking .... *Atarba* O. S. (p. 899)
Cross-vein *r* present 5
5. Anal angle of the wing prominent, almost square; *Rs* very elongate, straight; basal deflection of Cu_1 before the fork of *M* .... *Antocha* O. S. (p. 899)
Anal angle of the wing feeble; *Rs* shorter, more arcuated; basal deflection of Cu_1 at or beyond the fork of *M* 6
6. R_1 beyond the tip of *Sc* long, longer than the sector alone; veins issuing from cell *1st* M_2 very long .... *Dicranoptycha* O. S. (p. 900)
R_1 beyond the tip of *Sc* short, less than the length of the sector alone; veins issuing from cell *1st* M_2 short .... *Teucholabis* O. S. (p. 901)

The author's key to the Antochini given in Psyche (volume 20, pages 40–41, 1913) is erroneous in the disposition of Dicranoptycha, which runs down into the couplet with Atarba as having the radial cross-vein lacking. The key was based on material that was not normal and should be emended as above.

Genus **Rhamphidia** Meigen

1830 *Rhamphidia* Meig. Syst. Beschr., vol. 6, p. 281.

About eighteen species of the genus Rhamphidia are known, and they are distributed thruout all the major regions of the world. The larva of *Rhamphidia longirostris* (Palaearctic) has been found in the stems of

Rumex aquaticus. The two local species live in organic mud in swamps, and both the larvae and the pupae are decidedly eriopterine in appearance.

The local species of the genus Rhamphidia may be separated in accordance with the following key:

Rostrum short; legs yellow, tips of femora and tibiae black; wings tipped with dusky. [Dipt. Exot., 5th supp., p. 17. 1855. Osten Sacken, Mon. Dipt. N. Amer., part 4, p. 105–106. 1869.] (Plate XXXIII, 42.) .... *R. flavipes* Macq.
Rostrum long; legs uniformly dark brown; wings uniformly subhyaline, not tipped with dusky. [Proc. Acad. Nat. Sci. Phila., p. 498–499, pl. 25, fig. 14. 1916.] (Plate XXXIII, 43.) .... *R. mainensis* Alex.

Genus **Elephantomyia** Osten Sacken

1859 *Elephantomyia* O. S. Proc. Acad. Nat. Sci. Phila., p. 220.

The genus Elephantomyia includes about eight species, found in North America, Europe, Africa, and eastern Asia. The complete wing venation separates the flies from all other genera with an elongate rostrum, except the Oriental genus Rhampholimnobia Alex. The immature stages of the known species are spent in decaying wood.

Elephantomyia westwoodi O. S.

1869 *Elephantomyia westwoodi* O. S. Mon. Dipt. N. Amer., part 4, p. 109, pl. 1, fig. 5.

The species *Elephantomyia westwoodi* is a curious fly inhabiting cold Canadian woods and bogs, where it is found on the wing from late June into August. R. C. Shannon collected larvae at Washington in late November of 1912, and again on May 2, 1913, and reared the fly. It had been bred before by Johnson.

The adult is yellow with the abdominal segments ringed caudally with brown and the wings having a distinct brown stigma. The large square cell *1st* M_2 is a conspicuous feature of the venation (Plate XXXIII, 44).

Genus **Toxorhina** Loew

1835 *Limnobiorhynchus* Westw. Ann. Soc. Ent. France, vol. 4, p. 683.
1851 *Toxorhina* Loew. Linnaea Entomol., vol. 5, p. 400.
1869 *Toxorrhina* O. S. Mon. Dipt. N. Amer., part 4, p. 109–114.

The small genus Toxorhina includes about nine described species, most of which are from tropical America. The exceedingly reduced radial sector is the most interesting characteristic of the adult. The larval

life is spent presumably in damp earth, a very different habitat from that of the closely related genus Elephantomyia. The following key divides the local species:

Cell *1st* M_2 closed; body coloration brownish yellow; size, wing 6.5 mm. [*Toxorrhina magna* O. S. Proc. Ent. Soc. Phila., vol. 4, p. 232. 1865.] (Plate XXXIII, 45.) *T. magna* (O. S.)

Cell *1st* M_2 open by the atrophy of the medial cross-vein (closed in abnormal specimens only); body coloration gray; size smaller, wing less than 5.5 mm. [*Toxorrhina muliebris* O. S. Proc. Ent. Soc. Phila., p. 233. 1865.] (Plate XXXIII, 46.) .. *T. muliebris* (O. S.)

The small *T. muliebris* is northern in its distribution, while the larger *T. magna* is much more southern.

Genus **Atarba** Osten Sacken

1869 *Atarba* O. S. Mon. Dipt. N. Amer., part 4, p. 127–128.

A small number of species (about eight) are included in the genus Atarba, most of them belonging to tropical South America. In many of the species, including the local *A. picticornis*, the antennae of the male are elongated and beautifully annulated with yellow and brown. As has already been pointed out by the author a number of times, many of the species of crane-flies described by various workers as species of Atarba are in reality members of the aberrant eriopterine genus Gonomyia, subgenus Leiponeura (Alexander, 1916:508–509).

Atarba picticornis O. S.

1869 *Atarba picticornis* O. S. Mon. Dipt. N. Amer., part 4, p. 128–129, pl. 1, fig. 13.

Atarba picticornis is a rather common species, in suitable localities, flying in late June and July. The adult is reddish yellow; the antennae are yellow with the apical half of each flagellar segment dark brown; the abdomen is yellow with a black ring before the tip; the wings are pale yellow. *Sc* is short, the cross-vein *r* lacking; cell *1st* M_2 is small, with the basal deflection of Cu_1 inserted at its base (Plate XXXIII, 47).

Genus **Antocha** Osten Sacken

1859 *Antocha* O. S. Proc. Acad. Nat. Sci. Phila., p. 219.

The small genus Antocha includes about seven described species in the Northern Hemisphere. The immature stages are strictly aquatic, the pupae having branched pronotal breathing horns as in Simulium.

Both larvae and pupae live in cases on rocks, often in very rapid water, and the larvae are very pediciine in appearance. Mating takes place on the stones along the streams in which the larvae live.

Antocha saxicola O. S.

1859 *Antocha saxicola* O. S. Proc. Acad. Nat. Sci. Phila., p. 219.
1859 *Antocha opalizans* O. S. Proc. Acad. Nat. Sci. Phila., p. 220.

Antocha saxicola is a common fly, which may be mistaken only for a Dicranomyia but is readily distinguished by the very prominent anal angle of the wings (Plate XXXIII, 48), an uncommon feature in crane-flies. The milky-white color of the wings, and the very long, straight sector, are noteworthy characters. There are two distinct color phases which may represent distinct species when better known. The gray form has been described as *A. saxicola*, the red form as *A. opalizans*.

Genus **Dicranoptycha** Osten Sacken

1818 *Marginomyia* Meig. Syst. Beschr., vol. 1, p. 147.
1859 *Dicranoptycha* O. S. Proc. Acad. Nat. Sci. Phila., p. 217.

There are about nine described species of Dicranoptycha, six from North America, two from Europe, and one from Africa. *D. signaticollis* v. d. W. (of Java) is a Libnotes. The immature stages are spent in rather dry soil in open woods.

The following key separates the local species of Dicranoptycha:

1. Large, wing over 10 mm.; wings deep reddish brown, the veins with short golden hairs; *Rs* elongate, nearly twice the length of cell *1st* M_2. [Proc. Acad. Nat. Sci. Phila., p. 217. 1859.] (Plate XXXIII, 49.) . . . . *D. germana* O. S.
   Smaller, wing under 9 mm.; wings light gray or yellowish subhyaline; *Rs* shorter, about as long as or only slightly longer than cell *1st* M_2 2
2. Body coloration brownish gray; wings suffused with gray. [Proc. Acad. Nat. Sci. Phila., p. 218, pl. 4, fig. 13. 1859.] (Plate XXXIII, 51.) . . . . *D. sobrina* O. S.
   Body coloration pale yellow; wings pale yellow. [Proc. Acad. Nat. Sci. Phila., p. 500–501, pl. 25, fig. 12. 1916.] (Plate XXXIII, 50.) . . . . *D. winnemana* Alex.

There are three additional Austral species that may occur within the faunal limits considered by this paper. Of these, *Dicranoptycha nigripes* O. S. and *D. minima* Alex. have the tips of the femora blackened; *D. tigrina* Alex. resembles *D. sobrina*, but has the abdomen conspicuously cross-banded with brown and yellow, not uniformly brown as in *sobrina*.

A conspicuous feature occurring in the flies of this genus is the presence of a fold in the first anal cell of the wing, which is most evident if the wing is held against the light.

Genus **Teucholabis** Osten Sacken

1859 *Teucholabis* O. S. Proc. Acad. Nat. Sci. Phila., p. 222.

There are about forty-five described species in the genus Teucholabis, two-thirds of which are from tropical America, the center of distribution for the group. The larvae of *T. complexa* are found underneath decaying bark, a habitat very like that of the related genus Elephantomyia.

The local species of Teucholabis may be separated according to the following key:

Wing over 6 mm.; wings broad; *Sc* long, ending beyond two-thirds the length of the sector; *r* inserted on R_{2+3}; vein R_{2+3} not upturned at its tip, the end of cell *2d* R_1 being much broader than the end of cell R_3; prescutum reddish with three black stripes. [Proc. Acad. Nat. Sci. Phila., p. 223, pl. 3, fig. 10. 1859.] (Plate XXXIII, 52.) *T. complexa* O. S.

Smaller, wing under 5 mm.; wings narrow; *Sc* short, ending before midlength of the sector; *r* inserted at or near the end of *Rs*; vein R_{2+3} upturned at the tip, the end of cell R_3 being broader than the end of cell *2d* R_1; prescutum shiny black, only the humeral parts of the sclerite light yellow. [Can. Ent., vol. 48, p. 43. 1916. Proc. Acad. Nat. Sci. Phila., p. 498, pl. 25, fig. 16. 1916.] (Plate XXXIII, 53.)............ *T. lucida* Alex.

The vigorous, broad-winged *T. complexa* is the northernmost local species.

Tribe **Eriopterini**

The genera of the tribe Eriopterini may be separated in accordance with the following key:

1. Wings very much reduced, microscopic, very much smaller than the halteres. *Chionea* Dalman (p. 902)
   Wings normally developed, much longer than the halteres.......................... 2
2. Three branches of the media reaching the wing margin.......... *Cladura* O. S. (p. 903)
   Two branches of the media reaching the wing margin............................ 3
3. R_2 shorter than R_{2+3}.. 4
   R_2 longer than R_{2+3}... 7
4. Radial cross-vein present.. 5
   Radial cross-vein lacking.. 6
5. *Rs* elongate, longer than R_{4+5} alone; tuberculate pits on the anterior part of the prescutum.............................. *Rhabdomastix caudata* (Lundb.) (p. 904)
   Rs shorter, not so long as R_{4+5}; tuberculate pits retreated back on the prescutum. *Erioptera*, subgenus *Empeda* (p. 908)
6. *Sc* very long, extending to the end of the sector; basal deflection of Cu_1 at the fork of *M* or beyond.................................. *Rhabdomastix* Skuse (p. 904)
   Sc short, not extending beyond midlength of the sector; if *Sc* projects beyond the base of the sector, the basal deflection of Cu_1 is far before the fork of *M*. *Gonomyia* Meig. (p. 904)

7. *Rs* long, normal in position; cell *1st* R_1 elongated 8
   Rs shortened, its first fork with vein R_{2+3} at an angle to the end of the sector so that cell *1st* R_1 is equilateral or nearly so . . . . *Cryptolabis* O. S. (p. 906)
8. *Rs* ending in cell R_2 . . . . *Molophilus* Curt. (p. 906)
   Rs ending in cell R_3 9
9. A supernumerary cross-vein in cell R_2; second anal vein strongly bisinuate. *Helobia* St. Farg. (p. 907)
   No supernumerary cross-vein in cell R_2; second anal vein not bisinuate 10
10. Cu_1 tending to turn toward the wing apex; forks of the longitudinal veins very long and deep . . . . *Erioptera* Meig. (p. 908)
    Cu_1 straight or tending to turn away from the wing apex 11
11. Sides of the long cell *1st* M_2 parallel; Sc_2 not far removed from the tip of Sc_1; coloration of the local species black; basal deflection of Cu_1 beneath the middle of cell *1st* M_2. *Gnophomyia* O. S. (p. 909)
    Sides of cell *1st* M_2 more or less divergent distad; Sc_2 retreated toward the wing base so that Sc_1 is usually more than two-thirds the length of the sector 12
12. Deflection of Cu_1 meeting *M* far before the fork of the latter; *Rs* long and straight at its origin; the terminal three segments of the antennae abruptly smaller than the other segments of the flagellum; wings glabrous . . . . *Trimicra* O. S. (p. 910)
    Deflection of Cu_1 meeting *M* usually at the fork or on M_{3+4} underneath cell *1st* M_2; *Rs* shorter, tho straight; flagellar segments of the antennae gradually and uniformly smaller toward the tip of the organ; wings pubescent . . . . *Ormosia* Rond. (p. 911)

Genus **Chionea** Dalman

1816 *Chionea* Dalman. K. Vet. Akad. Handl., vol. 1, p. 102.

Chionea is a peculiar genus of subapterous crane-flies. There are about five European and six American species so far described. The possible evolution of the group from winged ancestors (Pterochionea Alex., Crypteria Berg.) has been discussed by the author in another paper (Alexander, 1916:529–530).

The immature stages of the known species are spent in the soil. The adult flies are usually found crawling about on the snow, being more conspicuous when snow is on the ground than at other seasons. In the spring and fall they are occasionally found in leaf mold. An interesting paper on the genus has been written by Johnson (1907). Dr. Dietz has in his collection a female specimen which was taken at Aweme, Manitoba, in September, when the temperature was below zero.

All the earlier authors describe this fly as being wingless. This is not exactly true, however, the wings being present tho reduced to mere knobs, much smaller than the halteres. The generalized species have the normal number of antennal segments for this tribe of flies, this being sixteen — the two scapal segments, a basal fusion segment of the flagellum made up of five segments, and nine free flagellar segments beyond. In the

specialized forms the number of free segments beyond the fusion segment is reduced to four or five, making a total of eleven or twelve segments.

The following key separates the local species of Chionea:

1. Color of the body grayish. [Can. Ent., vol. 49, p. 205-206. 1917.] *C. noveboracensis* Alex.
   Color of the body reddish yellow or yellow 2
2. Form long and slender, length of male less than 4 mm., diameter across thorax about 0.6 mm.; legs all very long and slender, not incrassated. [Can. Ent., vol. 49, p. 206. 1917.] .... *C. gracilis* Alex.
   Form stouter, length of male over 4 mm., diameter across thorax over 1 mm.; male with at least the posterior legs incrassated 3
3. Antennae with 12 segments, there being 9 flagellar segments beyond the 1st, or fusion, segment; all the femora incrassated; size larger, length of male about 5.5 mm., diameter across thorax 1.5 mm. [Can. Ent., vol. 49, p. 204-205. 1917.] ...... *C. primitiva* Alex.
   Antennae with 7 segments, there being 4 flagellar segments beyond the 1st, or fusion, segment; only the hind femora incrassated; size smaller, length of male about 5 mm., diameter across thorax 1 mm. [Ins. Injur. to Veget., 3d ed., p. 601, fig. 260. 1841.] *C. valga* Harr.
   (*C. scita* Walk. and *C. aspera* Walk. are probably synonymous with *C. valga*.)

Genus **Cladura** Osten Sacken

1859 *Cladura* O. S. Proc. Acad. Nat. Sci. Phila., p. 229.

There are but two described species of Cladura, both occurring within the limits considered in this paper. *Cladura fuscula* Loew (of Europe) is *Adelphomyia senilis* (Hal.); *C. flavescens* Brun. (of India) is doubtfully a member of this genus. It should be noted here that the antennae of Cladura have the basal segments of the flagellum united into a fusion-segment so that the antenna seems to have less than sixteen segments. The immature stages are quite unknown but are presumably spent in the soil.

The two species of Cladura are separated by the following key:

Large species, wing of female over 7 mm.; reddish yellow, the thoracic pleura spotted with brown; wings yellowish, the cross-veins and deflections of veins clouded with brown; *Sc* long, ending opposite the base of R_2, Sc_2 being about opposite the fork of R_{2+3}; *r* at or beyond one-third the length of R_2; petiole of cell M_1 short, not much longer than *m*. [*C. flavoferruginea* O. S., Proc. Acad. Nat. Sci. Phila., pl. 4, fig. 34, 1859. *C. indivisa* O. S., Proc. Acad. Nat. Sci. Phila., p. 291, 1861.] (Plate XXXVII, 102.) *C. flavoferruginea* O. S.

Smaller species, wing of female under 6 mm.; pale yellow, no spots on the thoracic pleura; wings hyaline without dark markings on the cross-veins and deflections of veins; *Sc* short, ending about opposite midlength of R_{2+3}, Sc_2 being nearly opposite the fork of the sector; *r* at about one-fourth the length of R_2; petiole of cell M_1 long, about twice the length of *m*. [Proc. Acad. Nat. Sci. Phila., p. 589-590, pl. 27, fig. 27. 1914.] (Plate XXXVII, 103.) *C. delicatula* Alex.

These species are characteristic late summer and autumnal crane-flies, very common in some localities thruout September and October. They

frequent open woodlands and shrubbery often remote from running water. *C. delicatula* is apparently a more local species than *C. flavoferruginea*, being more frequently found in mountainous localities.

It should be noted that *C. indivisa* is a synonym of *C. flavoferruginea* O. S. The remarkable variation in the venation of this species has been discussed by Alexander and Leonard (1912).

Genus **Rhabdomastix** Skuse

1889 *Rhabdomastix* Skuse. Proc. Linn. Soc. N. S. Wales, ser. 2, vol. 4, p. 829, pl. 22, fig. 15.

(Subgenus **Sacandaga** Alexander)

1911 *Sacandaga* Alex. Ent. News, vol. 22, p. 349–351.

Rhabdomastix is a small genus, including seven described species. The group is close to Gonomyia, but the male hypopygium has a very different structure and is of a distinctly primitive type. The subgenus Rhabdomastix, *sens. str.*, which occurs in Australia and South America, has greatly elongated antennae in the male sex; the subgenus Sacandaga, with four species and a race, has the antennae short in both sexes.

A key to the local species of Rhabdomastix follows:

Cross-vein *r* present tho weak; veins issuing from the small pentagonal cell *1st* M_2 subparallel; basal deflection of Cu_1 at the fork of M; body coloration grayish; arctic species. [*Goniomyia* (*Empeda*) *caudata* Lundb. Vidensk. Meddel. fra den naturh. Foren., p. 267, pl. 6, fig. 18. 1898.] (Plate XXXVI, 96.)........................*R. caudata* (Lundb.)

Cross-vein *r* lacking; veins issuing from the hexagonal cell *1st* M_2 arcuated; basal deflection of Cu_1 under the middle of cell *1st* M_2; body coloration yellowish. [*Sacandaga flava* Alex. Ent. News, vol. 22, p. 351–352, figs. 1–3. 1911.] (Plate XXXVI, 97.)...*R. flava* (Alex.).

Genus **Gonomyia** Meigen

1818 *Gonomyia* Meig. Syst. Beschr., vol. 1, p. 146.
1869 *Goniomyia* O. S. Mon. Dipt. N. Amer., part 4, p. 176.

In the genus Gonomyia there are about seventy-five described species, which are well distributed thruout the world, being found on all the continents and on many of the oceanic islands. The writer places the species in four subgenera — *Gonomyella* Alex., *Gonomyia* Meig., *Ptilostena* Bergr., and *Leiponeura* Skuse, the second and the fourth occurring within the limits considered in this paper. The coloration of many of the species is often contrasted brown and yellow, the pleura of the thorax being striped longitudinally. The immature stages of the species so far as

known are spent in wet earth or sand, and the larvae are of the usual elongate type of the Eriopterini.

The local species of Gonomyia may be separated according to the following key:

1. Two branches of the radial sector reaching the wing margin. (Subgenus *Leiponeura* Skuse.) 2
   Three branches of the radial sector reaching the wing margin.) Subgenus *Gonomyia* Meig.) 4
2. Outer deflection of vein M_3 absent, the cell *1st* M_2 being open; costa conspicuously china-white; legs banded with white. [*Elliptera alexanderi* Johns. Psyche, vol. 19, p. 3, fig. 6. 1912.] (Plate XXXVI, 86.) .... *G. alexanderi* (Johns.)
   Outer deflection of vein M_3 present, closing the cell *1st* M_2; costa not china-white; legs not banded with white 3
3. Pleural stripes conspicuous; stigma of the wings distinct; femora tipped with dark brown. [Proc. Acad. Nat. Sci. Phila., p. 587–588; pl. 27, fig. 25, wing; pl. 26, fig. 21, hypopygium. 1914.] (Plate XXXVI, 87.) .... *G. sacandaga* Alex.
   Pleural stripes lacking; no stigmal spot on the wings; femora not tipped with brown. [*Goniomyia manca* O. S. Mon. Dipt. N. Amer., part 4, p. 178–179. 1869.] (Plate XXXVI, 88.) .... *G. manca* (O. S.)
4. Basal deflection of Cu_1 far before the fork of M; subcosta long, ending beyond the origin of the sector 5
   Basal deflection of Cu_1 at or beyond the fork of M; subcosta short, ending opposite or before the origin of the sector 6
5. Wings clear, unspotted. [Ent. News, vol. 26, p. 170–172, figs. 1–3. 1915.] (Plate XXXVI, 89.) .... *G. mathesoni* Alex.
   Wings spotted. [Proc. Acad. Nat. Sci. Phila., p. 231, pl. 4, fig. 16. 1859.] (Plate XXXVI, 90.) .... *G. blanda* O. S.
6. Antennae orange at the base, the flagellum dark 7
   Antennae black thruout 9
7. Cell *1st* M_2 closed; femora with a dark brown subterminal ring. [Proc. Acad. Nat. Sci. Phila., p. 230. 1859.] (Plate XXXVI, 91.) .... *G. sulphurella* O. S.
   Cell *1st* M_2 open; femora without a dark subterminal ring 8
8. Male hypopygium with the dorsal angle of the pleurite stout, with numerous (about 15) slender hairs; ventral appendage simple, stout, tipped with a blunt black spine; second appendage a powerful, curved, subchitinized arm directed proximad. [Can. Ent., vol. 48, p. 316–317. 1916.] (Plate XXXVI, 92.) .... *G. florens* Alex.
   Male hypopygium with the dorsal angle of the pleurite slender, with a few (about 10) stout hairs; ventral appendage bifid, the arm with a long, slender, black spine at the tip; second appendage a slender, pale arm that is almost straight, and with two hairs at the tip. [Proc. Acad. Nat. Sci. Phila., p. 230, pl. 4, fig. 17. 1859.] (Plate XXXVI, 93.) .... *G. cognatella* O. S.
9. Subcosta short, ending before the origin of the sector, the distance between its tip and the origin of the sector being about equal to the *r-m* cross-vein; vein R_2 oblique, a little longer than the *r-m* cross-vein; male hypopygium with the gonapophyses and the penis guard fused into a large, prominent, cylindrical tube; thoracic pleura indistinctly striped. [Can. Ent., vol. 48, p. 319–320. 1916.] (Plate XXXVI, 94.] .... *G. noveboracensis* Alex.
   Subcosta longer, ending about opposite the origin of the sector; vein R_2 elongate; male hypopygium with the gonapophyses and the penis guard not fused into a cylindrical tube; thoracic pleura without stripes. [Proc. Acad. Nat. Sci. Phila., p. 231. 1859.] (Plate XXXVI, 95.) .... *G. subcinerea* O. S.

The above key is adapted from a revision of the American species of the genus by the author (Alexander, 1916: 508–528).

Genus **Cryptolabis** Osten Sacken

1859 *Cryptolabis* O. S. Proc. Acad. Nat. Sci. Phila., p. 224.

Cryptolabis is a small but well-defined genus, including three species, of which two are Nearctic and one is Neotropical. Nothing is known of the immature stages, but those of *C. paradoxa*, at least, are probably spent in moist earth.

Cryptolabis paradoxa O. S.

1859 *Cryptolabis paradoxa* O. S. Proc. Acad. Nat. Sci. Phila., p. 225, pl. 4, figs. 14, 15, 15 a.

The species *Cryptolabis paradoxa*, a curious little fly, is dark brown, with the dorso-pleural membranes and the root of the wings more yellowish; the whitish wings, with the apical cells pubescent and the sector short and straight or even slightly convex (Plate XXXVII, 101), easily distinguish the species. It is often rather common on rank herbage growing along wide creeks or on river banks. In these situations it may be swept in numbers from late June thruout July.

Genus **Molophilus** Curtis

1833 *Molophilus* Curt. Brit. Entomol., p. 444.

The genus Molophilus includes about forty-five described species, found in most parts of the world but better represented, apparently, in the temperate regions of both hemispheres. The immature stages so far as known are spent in moist earth.

The local species of Molophilus may be separated according to the following key:

1. Size very small, wing about 2.5 mm.; basal deflection of R_{2+3} short, perpendicular, about as long as the radial cross-vein; basal deflection of Cu_1 far before the fork of *M*. [*Erioptera ursina* O. S. Proc. Acad. Nat. Sci. Phila., p. 228. 1859.] (Plate XXXIV, 70.) . . . . *M. ursinus* (O. S.)
   Size larger, wing over 2.6 mm.; basal deflection of R_{2+3} longer, oblique; basal deflection of Cu_1 near the fork of *M* (as in *M. nova-caesariensis*) or beyond it on M_{3+4} . . . 2
2. Wings with a brown spot on the basal deflection of M_3. [*Erioptera comata* Doane. Journ. N. Y. Ent. Soc., vol. 8, p. 188, pl. 7, fig. 20. 1900.] (Plate XXXIV, 69.) *M. comatus* (Doane)
   Wings without such a brown spot 3
3. Antennae of the male elongated; coloration largely yellowish 4
   Antennae short in both sexes; coloration brown or blackish 5

4. Size small, wing under 5 mm.; bright yellow, the abdomen yellow; antennae of the female short. [*Erioptera pubipennis* O. S. Proc. Acad. Nat. Sci. Phila., p. 228. 1859.] (Plate XXXIV, 66.)..*M. pubipennis* (O. S.)
   Size larger, wing over 5.3 mm.; abdomen dark brown; antennae of the female longer. [Proc. Acad. Nat. Sci. Phila., p. 505–506, pl. 27, fig. 37. 1916.] (Plate XXXIV, 67.) *M. fultonensis* Alex.
5. Size small, wing under 3.5 mm.; basal deflection of Cu_1 near the fork of *M*. [Proc. Acad. Nat. Sci. Phila., p. 506–507, pl. 27, fig. 38. 1916.] (Plate XXXIV, 68.) *M. nova-caesariensis* Alex.
   Size larger, wing over 4 mm.; basal deflection of Cu_1 beyond the fork of *M* on M_{3+4}.....6
6. Antennae dark-colored; body coloration grayish brown. [*Erioptera hirtipennis* O. S. Proc. Acad. Nat. Sci. Phila., p. 228. 1859.] (Plate XXXIV, 65.) *M. hirtipennis* (O. S.)
   Antennae with the basal segments pale; body coloration pale brown. [*Erioptera forcipula* O. S. Mon. Dipt. N. Amer., part 4, p. 163. 1869.].............*M. forcipula* (O. S.)

The species identified above as being *M. comatus* may not belong to this species, which was described from western North America. The writer has seen only females (from Maine), but he has compared this material with Doane's types (also females) and cannot separate the material on the female sex.

Genus **Helobia** St. Fargeau et Serville

1825 *Helobia* St. Farg. et Serv. Encyclop. Method., Ins., vol. 10, p. 585.
1830 *Symplecta* Meig. Syst. Beschr., vol. 6, p. 282.
1865 *Idioneura* Phil. Verh. Zool.-Bot. Ges. Wien, vol. 15, p. 615.
1886 *Symplectomorpha* Mik. Wien. Ent. Zeitung, vol. 5, p. 318.

In the genus Helobia there are four described species, one of which, the local *H. hybrida*, is probably the most widely distributed of all crane-flies, ranging from India over Europe and Asia, thruout North America, and southward along the Andes to Chile and Argentina. Future collecting will undoubtedly extend the range even more. The immature stages are spent in moist earth and sand.

Helobia hybrida (Meig.)

1804 *Limonia hybrida* Meig. Klass., vol. 1, p. 57, pl. 3, fig. 17.
1818 *Limnobia punctipennis* Meig. Syst. Beschr., vol. 1, p. 147, pl. 5, figs. 2, 3, 7.
1848 *Limnobia cana* Walk. List Dipt. Brit. Mus., vol. 1, p. 48.

Helobia hybrida is a grayish fly, with three brown stripes on the prescutum; the wings are whitish, with a supernumerary cross-vein in cell R_2 and the second anal vein curiously bisinuate (Plate XXXVII, 98). The species is common everywhere. It is the earliest of the vernal

crane-fly fauna, appearing on the wing in March. It is seen most commonly in spring and autumn, and is less numerous in July. It is presumably double-brooded.

Genus **Erioptera** Meigen

1800 *Polymeda* Meig. Nouv. Class. Mouch., p. 14 (*nomen nudum*).
1803 *Erioptera* Meig. Illiger's Mag., vol. 2, p. 262.
1856 *Chemalida* Rond. Prodromus, vol. 1, p. 180.
1856 *Limnaea* Rond. Prodromus, vol. 1, p. 181.
1861 *Limnoica* Rond. Prodromus, vol. 4, Corrigenda, p. 11.

The rather extensive genus Erioptera includes about ninety described species, most numerous in the Northern Hemisphere. The immature stages of the known species are spent in damp earth. The local species are distributed in five subgenera, separated by the following key:

1. Second anal vein arcuated so that cell *1st A* is as broad at the middle as, or broader than, at the margin; cross-vein *m* absent, cell *1st* M_2 opening into cell M_2. . . . . *Erioptera* Meig.
Anal veins divergent, cell *1st A* being broadest at the margin; cell *1st* M_2 closed, if open the outer deflection of M_3 lacking, cell *1st* M_2 opening into cell M_3 (except in Empeda) 2
2. Fork of cell R_2 short, about as long as its petiole (R_{2+3}); Sc_1 short . . . . *Empeda* O. S.
Fork of cell R_2 long, at least four times as long as its petiole (R_{2+3}); Sc_1 longer. 3
3. Cell *1st* M_2 open, the outer deflection of M_3 atrophied; if closed, the cross-vein *m* and the deflection of M_3 about on a line . . . . *Mesocyphona* O. S.
Cell 1st M_2 closed 4
4. A spur from the outer deflection of M_3 jutting into cell *1st* M_2. . . . . *Hoplolabis* O. S.
No spur from M_3 jutting into cell *1st* M_2. . . . . *Acyphona* O. S.

The following key divides the local species of Erioptera:

1. Cell *1st* M_2 open by the atrophy of the outer deflection of M_3. (Subgenus *Mesocyphona*.) 2
Cell *1st* M_2 closed; if open, it is by the atrophy of the medial cross-vein 4
2. Wings pale gray, with small brown dots at the tips of the veins along the margins. [Proc. Acad. Nat. Sci. Phila., p. 227. 1859.] (Plate XXXV, 79.). . . . . *E. parva* O. S.
Wings grayish or brown, with white dots and spots. 3
3. Wings with abundant white dots in all the cells; each femur with two brown rings. [Journ. Acad. Nat. Sci. Phila., vol. 3, p. 17. 1823.] (Plate XXXV, 77.) *E. caloptera* Say
Wings with about twenty large spots that are confined to the region of the veins; each femur with a single brown ring before the tip. [Can. Ent., vol. 50, p. 383–384. 1918.] (Plate XXXV, 78.). . . . . *E. needhami* Alex.
4. Cell *1st* M_2 open by the atrophy of *m*; second anal vein arcuated, before its tip bent strongly toward the first so that cell *1st A* at its middle is about as broad as or broader than at the margin. (Subgenus *Erioptera*.) (See also *E.* [*Empeda*] *stigmatica*, below.) .5
Cell *1st* M_2 closed; anal veins divergent 10
5. Knobs of the halteres dark brown. [Proc. Acad. Nat. Sci. Phila., p. 226. 1859.] (Plate XXXV, 72.). . . . . *E. septemtrionis* O. S.
Knobs of the halteres pale. 6

6. Body and wings dark brown. [Proc. Acad. Nat. Sci. Phila., p. 226. 1859.] (Plate XXXV, 71.) .... *E. villosa* O. S.
   Body and wings yellow or green 7
7. Wings yellowish, the cross-veins and deflections of veins with tiny brown dots. [Proc. Acad. Nat. Sci. Phila., p. 226. 1859.] (Plate XXXV, 74.) .... *E. chrysocoma* O. S.
   Wings yellowish or green, unmarked 8
8. Thorax reddish, the humeral parts of the mesonotum yellow; eyes of the male conspicuously enlarged. [Proc. Acad. Nat. Sci. Phila., p. 226, pl. 4, fig. 19. 1859.] (Plate XXXV, 73.) .... *E. vespertina* O. S.
   (*E. megophthalma* Alex. [Can. Ent., vol. 50, p. 60–61, 1918], described since the above was written, is entirely reddish without the yellow humeral angles to the thorax.)
   Thorax pale green or yellow; eyes of both sexes normal 9
9. Coloration of body and wings pale green. [Proc. Acad. Nat. Sci. Phila., p. 226. 1859.] (Plate XXXV, 75.) .... *E. chlorophylla* O. S.
   Coloration of body and wings pale yellow. [Mon. Dipt. N. Amer., part 4, p. 157. 1869.] (Plate XXXV, 76.) .... *E. straminea* O. S.
10. Cell R_2 short, about as long as R_{2+3} alone. (Subgenus *Empeda*.) 11
    Cell R_2 deep, much longer than R_{2+3} alone 12
11. Cell *1st* M_2 closed. [Proc. Acad. Nat. Sci. Phila., p. 503–505, pl. 27, fig. 36. 1916.] (Plate XXXV, 84.) .... *E. nyctops* Alex.
    Cell *1st* M_2 open. [*Empeda stigmatica* O. S. Mon. Dipt. N. Amer., part 4, p. 184. 1869.] (Plate XXXV, 85.) .... *E. stigmatica* (O. S.)
12. A stump of a vein in cell *1st* M_2; no brown bands on the femora. (Subgenus *Hoplolabis*.) [Proc. Acad. Nat. Sci. Phila., p. 227, pl. 4, figs. 20, 21. 1859.] (Plate XXXV, 83.) *E. armata* O. S.
    No stump of a vein in cell *1st* M_2; femora banded with brown. (Subgenus *Acyphona*.) .. 13
13. Wings with a broad brown band at the cord and a large brown basal spot. [Proc. Acad. Nat. Sci. Phila., p. 227, pl. 4, fig. 23. 1859.] (Plate XXXV, 80.) .... *E. venusta* O. S.
    Wings not so marked 14
14. Coloration of body and wings more yellowish; an uninterrupted brown band along the cord; brown bands on the femora less extensive, the yellow area between them broad; basal deflection of Cu_1 at the fork of M. [Mon. Dipt. N. Amer., part 4, p. 158. 1869.] (Plate XXXV, 81.) .... *E. armillaris* O. S.
    Coloration of body and wings more brownish, the markings on the wings less extensive and the band on the cord interrupted; bands on the femora very extensive, the yellowish area between them very narrow; basal deflection of Cu_1 before the fork of M. [Proc. Acad. Nat. Sci. Phila., p. 227. 1859.] (Plate XXXV, 82.) .... *E. graphica* O. S.

Erioptera (*Empeda*) *noctivagans* Alex. (Alexander, 1917:200–201), from Virginia, has been described since the completion of the above key. It is closest to *E. stigmatica*, but is larger and darker, the wing veins are dark brown with an indistinct darker seam along the cord, and the three pleural appendages of the male hypopygium are very unequal in length, the shortest being less than two-thirds the length of the longest and conspicuously bifid at its apex. The very long verticils of the antennae in the subgenus Empeda are present, but are less conspicuous than in *E. stigmatica*.

Genus **Gnophomyia** Osten Sacken

1859 *Gnophomyia* O. S. Proc. Acad. Nat. Sci. Phila., p. 223.
1867 *Furina* Jaenn. Abhandl. Senkenb. Ges., vol. 6, p. 318.

The genus Gnophomyia includes about twenty-eight species of medium-sized to comparatively large flies, mostly from tropical America. The immature stages so far as known are spent beneath the decaying bark of deciduous trees (Liriodendron, Populus, Acer, and others).

Gnophomyia tristissima O. S.

1859 *Gnophomyia tristissima* O. S. Proc. Acad. Nat. Sci. Phila., p. 224, pl. 4, fig. 18.

Gnophomyia tristissima is a rather small blackish fly, with dark wings and the knobs of the halteres bright yellow. The venation is as shown in Plate XXXVII, 100.

A second species of the genus, *Gnophomyia luctuosa* O. S. (Proc. Acad. Nat. Sci. Phila., p. 224, 1859), has recently been taken near Washington, D. C., by Mr. Shannon. It is a southern species, with a wide range over Central America and northern South America. It may be readily distinguished from *G. tristissima* by its stouter build, entirely black halteres, and apically pubescent wings.

Genus **Trimicra** Osten Sacken

1861 *Trimicra* O. S. Proc. Acad. Nat. Sci. Phila., p. 290.

The genus Trimicra includes about fourteen described species of rather inconspicuously colored flies of medium size. The species are found in all the principal regions of the globe, including many of the oceanic islands. The genotype, *Trimicra anomala*, was later considered by its describer as being the same as the European *T. pilipes* Fabr., but the two should be regarded as being distinct species until the question can be settled by the study of ample material. The immature stages are spent in moist earth.

Trimicra anomala O. S.

1861 *Trimicra anomala* O. S. Proc. Acad. Nat. Sci. Phila., p. 290.

Trimicra anomala is a brownish gray fly. The prescutum has three dark brown stripes, and the abdominal segments are margined laterally and caudally with paler. The wings (Plate XXXVII, 99) are suffused with pale brown, the cross-veins being a little darker. The legs and the body are clothed with long, erect hairs. The species is more numerous southward and westward.

Genus **Ormosia** Rondani

1856 *Ormosia* Rond. Prodromus, vol. 1, p. 180.
1856 *Ilisomyia* Rond. Prodromus, vol. 1, p. 180.
1860 *Rhypholophus* Kol. Wien. Ent. Monatschr., vol. 4, p. 393.
1863 *Dasyptera* Schin. Wien. Ent. Monatschr., vol. 7, p. 221.

The genus Ormosia includes about sixty-two described species, of temperate zones, almost all occurring in the temperate regions of Europe and North America. The immature stages are spent in mud and damp earth.

The local species of Ormosia may be separated in accordance with the following key:

1. Wings spotted or clouded with darker 2
Wings unicolorous or nearly so, the stigma only being darker 5
2. Anal veins divergent; wing markings produced by actual dark brown spots and blotches 3
Anal veins convergent, the second anal vein before its tip bent strongly toward the first; wing markings produced by dark-colored hairs on pale brown clouds 4
3. Wings with brown dots in all the cells. [*Rhypholophus innocens* O. S. Mon. Dipt. N. Amer., part 4, p. 142. 1869.] (Plate XXXIV, 56.) . . . . . *O. innocens* (O. S.)
Wings with three brown costal spots, the cord margined with brown, the base and the apex of the wing darkened. [Psyche, vol. 18, p. 200–201, pl. 16, fig. 6. 1911.] (Plate XXXIV, 55.) . . . . . *O. apicalis* Alex.
(*O. atriceps* Dietz [Trans. Amer. Ent. Soc., vol. 42, p. 136–137, pl. 10, figs. 1 and 2, 1916] is apparently too close to *O. apicalis* to be separated therefrom.)
4. An indistinct crossband along the cord. [*Erioptera fascipennis* Zett. Ins. Lapponica, Dipt., p. 831. 1838.] . . . . . *O. fascipennis* (Zett.)
Wings with three or four indistinct grayish crossbands. [*Erioptera nubila* O. S. Proc. Acad. Nat. Sci. Phila., p. 227. 1859.] (Plate XXXIV, 54.) . . . . . *O. nubila* (O. S.)
5. Cell *1st* M_2 closed 6
Cell *1st* M_2 open 10
6. Anal veins divergent 7
Second anal vein arcuated, before its tip bent strongly toward the first. [*Rhypholophus arcuatus* Doane. Ent. News, vol. 19, p. 201. 1908.] . . . . . *O. arcuata* (Doane)
7. Antennae entirely brown; thorax reddish brown, shining; basal deflection of Cu_1 under the middle of cell *1st* M_2. [Trans. Amer. Ent. Soc., vol. 42, p. 137–138, pl. 10, fig. 3. 1916.] . . . . . *O. abnormis* Dietz
Not colored as above; basal deflection of Cu_1 before or at the fork of M 8
8. Entire thorax and coxae yellowish red; antennae pale yellowish, darkened toward the tip. [Trans. Amer. Ent. Soc., vol. 42, p. 138–139, pl. 10, fig. 4. 1916.] *O. luteola* Dietz
Thorax not colored as above 9
9. Mesonotum reddish with a median brown line which in some cases is indistinct; antennae pale thruout or with only the extreme tip darkened. [*Trimicra pygmaea* Alex. Psyche, vol. 19, p. 166, pl. 13, fig. 3. 1912.] (Plate XXXIV, 58.) . . . . . *O. pygmaea* (Alex.)
(*O. pilosa* Dietz is the same as *O. pygmaea*.)
Mesonotum brownish gray; the four basal antennal segments yellow. [*Rhypholophus nigripilus* O. S. Mon. Dipt. N. Amer., part 4, p. 142. 1869.] (Plate XXXIV, 57.) *O. nigripila* (O. S.)
10. Medial cross-vein lacking, cell *1st* M_2 confluent with cell M_2 11
Outer deflection of M_3 lacking, cell *1st* M_2 confluent with cell M_3 12

11. Second anal vein arcuated, before its tip bent strongly toward the first. [*Erioptera holotricha* O. S. Proc. Acad. Nat. Sci. Phila., p. 226. 1859.]....*O. holotricha* (O. S.)
Anal veins divergent. [Trans. Amer. Ent. Soc., vol. 42, p. 140, pl. 10, fig. 6. 1916.] *O. palpalis* Dietz
12. Antennae of both sexes shorter than the thorax....................13
Antennae of the male approximately as long as the whole body, beadlike in structure....................19
13. Second anal vein arcuated, before its tip bent strongly toward the first..........14
Anal veins divergent....................18
14. Thorax reddish....................15
Thorax not reddish....................16
15. Mesonotum with a dark median line; male hypopygium with two pleural appendages which are almost straight; gonapophyses elongate, black, profoundly bifid; penis guard not trifid. [*Rhypholophus rubellus* O. S. Mon. Dipt. N. Amer., part 4, p. 144, pl. 1, fig. 15. 1869.] (Plate XXXIV, 60.)..........*O. rubella* (O. S.)
Mesonotum without a dark median line; male hypopygium with the pleural appendage a single curved hook; gonapophyses strongly curved, entire hooks; penis guard trifid at apex. [Can. Ent., vol. 49, p. 24–25. 1917.] (Plate XXXIV, 59.) *O. nimbipennis* Alex.
16. Stigma distinct, dark brown, the marking continued down onto the cord. [*Erioptera meigenii* O. S. Proc. Acad. Nat. Sci. Phila., p. 226. 1859.] (Plate XXXIV, 61.) *O. meigenii* (O. S.)
Stigma indistinct or lacking....................17
17. Thorax and antennae light yellow. [*Rhypholophus parallelus* Doane. Ent. News, vol. 19, p. 202. 1908.]..........*O. parallela* (Doane)
Thorax brown, with a grayish pruinosity and a rather broad darker stripe; antennae brown. [Trans. Amer. Ent. Soc., vol. 42, p. 141. 1916.]..........*O. perplexa* Dietz
18. Mesonotum with a darker line on either side; ninth sternite produced into a median spatulate lobe. [Trans. Amer. Ent. Soc., vol. 42, p. 142–143, pl. 10, fig. 8. 1916.] *O. bilineata* Dietz
Mesonotum reddish brown with a median brown stripe; ninth sternite produced into two flattened lobes that project far caudad. [Trans. Amer. Ent. Soc., vol. 42, p. 143–144, pl. 10, fig. 9. 1916.]..........*O. deviata* Dietz
19. Anal veins convergent....................20
Anal veins divergent....................21
20. Segments of flagellum shorter, without pale apices. [Can. Ent., vol. 49, p. 25. 1917.] (Plate XXXIV, 63.)..........*O. mesocera* Alex.
Antennal segments elongated, the segments attenuated and the apices pale. [*Rhypholophus monticola* O. S. Mon. Dipt. N. Amer., part 4, p. 145. 1869.] (Plate XXXIV, 62.)..........*O. monticola* (O. S.)
21. Reddish brown; mesonotum with an indistinct brown median stripe. [Trans. Amer. Ent. Soc., vol. 42, p. 144–145, pl. 10, fig. 10. 1916.]..........*O. divergens* Dietz
Dark brown; mesonotum with three darker brown stripes. [Can. Ent., vol. 49, p. 26. 1917.] (Plate XXXIV, 64.)..........*O. megacera* Alex.
(*O. megacera* is probably the same as *O. divergens*, the latter name preoccupied by *O. divergens* Coq. [1905].)

The small flies that make up this characteristic genus are very common, appearing in small swarms under overhanging ledges, along the lower face of an inclined tree, or in similar situations. The early spring species are *Ormosia innocens*, *O. nubila*, *O. meigenii*, *O. holotricha*, and others; *O. apicalis*, *O. megacera*, and *O. mesocera* occur in early summer; *O. nigripila*, *O. nimbipennis*, *O. monticola*, and *O. abnormis* are late

summer species. *O. rubella* has a long flight period, from June to September, and some of the early spring species (as *O. nubila* and *O. meigenii*) reappear in the late summer and in the autumn, apparently being double-brooded.

Tribe **Limnophilini**

The genera of the tribe Limnophilini may be separated according to the following key:

1. Sc_2 before the origin of the sector; antennae 17-segmented; wings pubescent. *Ula* Hal. (p. 913)
   Sc_2 beyond the origin of the sector; antennae 16-segmented (apparently with fewer segments in *Adelphomyia cayuga*) 2
2. Wings pubescent, at least apically 3
   Wings glabrous or with microscopic pubescence only 5
3. Pubescence including the entire wing; cell M_1 absent . . . . . *Ulomorpha* O. S. (p. 913)
   Pubescence only on the apical cells of the wing; cell M_1 present or lacking 4
4. Small species, wing less than 5.5 mm.; male antennae short . . *Adelphomyia* Bergr. (p. 914)
   Larger species, wing over 6 mm.; male antennae elongated. *Limnophila*, subgenus *Lasiomastix* O. S. (p. 916)
5. A supernumerary cross-vein in cell C . . . . . *Epiphragma* O. S. (p. 914)
   No supernumerary cross-vein in cell C . . . . . *Limnophila* Macq. (p. 915)

Genus **Ula** Haliday

1833 *Ula* Hal. Ent. Mag., vol. 1, p. 153.
1864 *Macroptera* Lioy. Atti dell' Institut Veneto, ser. 3, vol. 9, p. 224.

The small genus Ula includes about six described species, all being Holarctic except one species from Java. The larval stages of the known species are spent in fungi (Alexander, 1915 a: 1–8). The species are subject to considerable variation in the wing pattern, but it now seems that in eastern America there are at least two species, which are divided by the following key:

Antennae elongate in the male; wings dusky, but without a heavy brown pattern. [Mon. Dipt. N. Amer., part 4, p. 277. 1869.] . . . . . *U. paupera* O. S.
Antennae short in both sexes; wings with the cord and outer end of cell *1st* M_2 seamed with brown. [Mon. Dipt. N. Amer., part 4, p. 276. 1869.] (Plate XLI, 164.) *U. elegans* O. S.

Genus **Ulomorpha** Osten Sacken

1869 *Ulomorpha* O. S. Mon. Dipt. N. Amer., part 4, p. 232.

In the genus Ulomorpha there is but a single described species, agreeing superficially with Ula in the entirely pubescent wings but with Sc_2 close at the tip of Sc_1. The immature stages are in rich organic earth, and are

very different from those of Ula and closer to those of the subgenus Lasiomastix in the genus Limnophila.

Ulomorpha pilosella (O. S.)

1859 *Limnophila pilosella* O. S. Proc. Acad. Nat. Sci. Phila., p. 241.
1869 *Ulomorpha pilosella* O. S. Mon. Dipt. N. Amer., part 4, p. 233.

Ulomorpha pilosella is a shiny, reddish brown fly, with the wings faintly darkened. The sessile or subsessile cell R_2 is a well-marked feature of the venation (Plate XLI, 163). The insect is common in cold Canadian woods thruout northeastern North America.

Genus **Adelphomyia** Bergroth

1891 *Adelphomyia* Bergr. Mittheil. Naturf. Ges. Bern, 1890, p. 134.

The species of the genus Adelphomyia are among the smallest of the Limnophilini. The immature stages of the American species are spent in rich, saturated, organic earth in shady situations. There are two European and three American species thus far described. *Adelphomyia cayuga* and *A. americana* are commonest in late summer; *A. minuta* is a species of late spring and early summer, fairly common in rich Canadian woods, in gorges, and near wooded bogs.

A recent study of the larval head in this genus shows a decided relationship with the tribe Pediciini, and it seems probable that the genus will have to be placed in that tribe despite the very limnophiline appearance of the adults.

The local species of Adelphomyia may be separated by the following key:

1. Cell M_1 of wings lacking; coloration of body dark brown; antennae with less than 16 segments, the basal segments of the flagellum fused together. [Pomona Journ., vol. 4, p. 831, fig. B. 1912.] (Plate XLI, 162.) . . . . *A. cayuga* Alex.
   Cell M_1 of wings present; coloration of body yellow or light yellowish brown; antennae with the basal flagellar segments distinct 2
2. Pubescence in cells of wings sparse; cross-vein *r* not evident; cross-vein *m* short or obliterated by fusion of M_3 on M_{1+2}; color of body light yellow. [Can. Ent., vol. 43, p. 287–288. 1911.] (Plate XLI, 161.) . . . . *A. minuta* Alex.
   Pubescence in cells of wings conspicuous; cross-veins *r* and *m* usually distinct, the former in some cases little evident; color of body yellowish brown. [Pomona Journ., vol. 4, p. 829–830, fig. A. 1912. Ent. News, vol. 22, p. 353–354, fig. 4, as *A. senilis* Hal. of Europe. 1911.] (Plate XLI, 160.) . . . . *A. americana* Alex.

Genus **Epiphragma** Osten Sacken

1859 *Epiphragma* O. S. Proc. Acad. Nat. Sci. Phila., p. 238.

Epiphragma is a small genus of handsome flies including about eighteen described species, which are most abundant in the tropics of America. The flies are of medium size and are among the most beautiful in the family, their wing pattern of ocellate spots and bands producing a striking effect. The immature stages are amphibious, the larval life being spent in saturated decaying wood such as ash (Fraxinus) and buttonbush (Cephalanthus), in swampy situations, and in similar habitats.

The following key divides the local species:

Wings with pale brown crossbands which are margined with darker; a brown annulus at the tip of each femur. [*Limnobia fascipennis* Say. Journ. Acad. Nat. Sci. Phila., vol. 3, p. 19. 1823.] (Plate XLI, 158.) .... *E. fascipennis* (Say)
Wings with an irregular pattern of brown and tawny; a brown annulus before the tip of each femur. [*Limnophila solatrix* O. S. Proc. Acad. Nat. Sci. Phila., p. 238. 1859.] (Plate XLI, 159.) .... *E. solatrix* (O. S.)

In many specimens of *Epiphragma fascipennis* the wing bands are more continuous than in the wing shown, there being usually three such bands, the last lying across the wing tip distad of the cord. The wing pattern is strongly suggestive of that of the rare primitive tanyderid *Protoplasa fitchii*, and most of the specimens of the latter that have been located in museums were found pinned among series of *Epiphragma fascipennis*.

Genus **Limnophila** Macquart

1834 *Limnophila* Macq. Suit. à Buff., vol. 1, Hist. Nat. Ins., Dipt., p. 95.
1861 *Limnomya* Rond. Prodromus, vol. 4, Corrigenda, p. 11.
1888 *Pilaria* Sintenis. Sitzber. Nat.-Ges. Dorpat., vol. 8, p. 398.

Limnophila is one of the largest of the crane-fly genera, the number of described species being between one hundred and ninety and two hundred, of which a quarter occur within the geographical limits considered in this paper. The subgenera into which the genus is divided are here recognized largely for convenience only, some of them being poorly definable. The larval and pupal characters will be found to be much more valuable in delimiting these groups. *Limnophila mundoides* and *L. emmelina* both represent groups which are as well defined as the sub-genera here recognized. Most of the forms of northeastern North America fly during the month of June and are to be found in cold Canadian woodlands. The immature stages of most species of Limnophila are spent in rich, saturated mud or earth.

The local species of Limnophila may be separated in accordance with the following key:

1. Cell M_1 of the wings present 2
   Cell M_1 of the wings lacking 41
2. A supernumerary cross-vein in cell R_2 or in cell M 3
   No supernumerary cross-vein in cell R_2 or in cell M 6
3. A supernumerary cross-vein in cell M 4
   A supernumerary cross-vein in cell R_2. (Subgenus *Dicranophragma* O. S.) [Proc. Acad. Nat. Sci. Phila., p. 240. 1859.] (Plate XXXIX, 139.) . . . . *L. fuscovaria* O. S.
4. Wings interruptedly crossbanded with brown; costal region without equidistant brown blotches; *Rs* spurred at the bend; antennae of male elongated. (Subgenus *Idioptera* Macq.) [Mon. Dipt. N. Amer., part 4, p. 206. 1869.] (Plate XXXVIII, 115.) *L. fasciolata* O. S.
   Wings hyaline or spotted with brown; *Rs* slightly or not at all spurred at the bend; antennae of male short. (Subgenus *Ephelia* Schin.) 5
5. Wings hyaline. [Proc. Acad. Nat. Sci. Phila., p. 591, pl. 25, fig. 2. 1914.] (Plate XXXIX, 138.) . . . . *L. johnsoni* Alex.
   Wings spotted; a series of about 6 or 7 large brown blotches along the costal margin. [Proc. Acad. Nat. Sci. Phila., p. 235, pl. 4, fig. 25. 1859.] (Plate XXXIX, 137.) *L. aprilina* O. S.
6. Apical cells of wings pubescent; antennae of male elongated. (Subgenus *Lasiomastix* O. S.) 7
   Apical cells of wings not pubescent 8
7. Thorax shiny black; wings banded with brown. [*Limnobia macrocera* Say. Journ. Acad. Nat. Sci. Phila., vol. 3, p. 20. 1823.] (Plate XXXVIII, 113.) *L. macrocera* (Say)
   Thorax dark gray; wings unmarked. [Mon. Dipt. N. Amer., part 4, p. 208. 1869.] (Plate XXXVIII, 117.) . . . . *L. tenuicornis* O. S.
   (*L. subtenuicornis* Alex. [Can. Ent., vol. 50, p. 61–62, 1918], described since this key was made, has cell M_1 lacking. It is a member of the subgenus Lasiomastix and is readily distinguished by the combination of pubescent wings and lack of cell M_1. There can be no doubt that *L. tenuicornis* and *L. subtenuicornis* should be coupled with *L. macrocera* in the subgenus *Lasiomastix*, both being notable by the distinct pubescence in the apical cells of the wings.)
8. Thorax shiny black 9
   Thorax not shiny black 10
9. Wings with a brownish tinge; femora dull brownish yellow, narrowly tipped with dark brown; legs stout, conspicuously hairy; male hypopygium of the normal simple limnophiline structure. (Subgenus *Prionolabis* O. S.) [Mon. Dipt. N. Amer., part 4, p. 226. 1869.] (Plate XL, 144.) . . . . *L. munda* O. S.
   Wings hyaline or nearly so; femora dark brown, only the extreme bases paler; legs slender, not conspicuously hairy; male hypopygium complex in structure. [Journ. N. Y. Ent. Soc., vol. 24, p. 120–121, pl. 8, fig. 3. 1916.] (Plate XL, 145.) *L. mundoides* Alex.
10. Hind tarsi white; antennae of male elongated 11
    Hind tarsi not white 12
11. Thorax black with a gray bloom; R_{2+3} about equal to or slightly longer than the basal deflection of Cu_1. [Mon. Dipt. N. Amer., part 4, p. 209. 1869.] (Plate XXXVIII, 118.) . . . . *L. niveitarsis* O. S.
    Thorax reddish yellow; R_{2+3} about twice as long as the basal deflection of Cu_1. [Ent. News, vol. 24, p. 248–249, fig. 1913.] (Plate XXXVIII, 119.) . . . . . *L. albipes* Leon.

Cross-vein r removed some distance from the tip of R_1, so that this distance is from one and one-half to two times the length of the radial cross-vein; tuberculate pits present........13

Ultimate segment of R_1 curved to the costa and scarcely longer than the cross-vein r itself; tuberculate pits lacking in all species except *fratria*........22

(*L. marchandi* should be interpreted as coming in this division, from the evident relationship with *L. alleni.*)

Cell *1st* M_2 very much elongated, the inner end lying far inside the level of the cord. [Proc. Acad. Nat. Sci. Phila., p. 237. 1859.] (Plate XXXVIII, 124.) *L. areolata* O. S.

Cell *1st* M_2 not greatly elongated, the inner end at the level of the cord........14

R_{2+3} longer than cell R_2 alone. [Proc. Acad. Nat. Sci. Phila., p. 238, pl. 4, fig. 26. 1859.] (Plate XXXVIII, 127.)........*L. ultima* O. S.

R_{2+3} not longer than cell R_2 alone........15

Cell M_1 very short, not longer than the basal deflection of Cu_1. [Proc. Acad. Nat. Sci. Phila., p. 237. 1859.] (Plate XXXVIII, 125.)........*L. brevifurca* O. S.

(Specimens of *L. brevifurca* are rather frequently found in which the fusion of M_{1+2} is continued to the wing margin, in which case the species would run down to couplet 41; such abnormal specimens are rare, however, and usually have one of the wings normal.)

Cell M_1 long, more than twice as long as the basal deflection of Cu_1........16

Head narrow, prolonged behind; cells R_3 and *1st* M_2 longer than cell R_5, so that the cord is not in a straight line; radial and medial veins long, slender, arcuated; second anal vein incurved at the tip. (Subgenus *Pseudolimnophila* Alex.)........17

Head broad, not narrowed behind; cells R_3, R_5, and *1st* M_2 with their inner ends about on a level; radial and medial veins stout and straight; second anal vein not incurved at the tip. (Subgenus *Eulimnophila* Alex.)........20

Wings with small brown dots on the cross-veins and at the forks. [Proc. Acad. Nat. Sci. Phila., p. 236, pl. 4, fig. 24. 1859.] (Plate XXXIX, 135.)....*L. luteipennis* O. S.

Wings clear, unspotted........18

Thorax clear blue-gray. [Mon. Dipt. N. Amer., part 4, p. 219. 1869.] (Plate XXXIX, 134.)........*L. inornata* O. S.

Thorax brownish without gray color........19

Pleura of thorax grayish, unmarked; size small. [Mon. Dipt. N. Amer., part 4, p. 218. 1869.]........*L. contempta* O. S.

Pleura of thorax dull yellow, with a conspicuous dark brown stripe extending from the cervical sclerites to the postnotum; size larger. [Proc. Acad. Nat. Sci. Phila., p. 592, pl. 25, fig. 3. 1914.] (Plate XXXIX, 136.)........*L. nigripleura* A. & L.

(In the writer's key to the species of the *luteipennis* group [Proc. Acad. Nat. Sci. Phila., p. 593, 1914], in couplet 4 *L. contempta* is given as being a larger species than *L. nigripleura.* This is erroneous, *L. contempta* being the smallest species of the group. It is more southern in its distribution than *L. nigripleura.*)

Wings narrow, grayish; stigma distinct, hairy; antennae of male elongated. [*Limnobia tenuipes* Say. Journ. Acad. Nat. Sci. Phila., vol. 3, p. 21. 1823.] (Plate XXXVIII, 121.)........*L. tenuipes* (Say)

Wings broader, more yellowish brown; stigma not distinct; antennae of male short....21

Body opaque; front gray. [Proc. Acad. Nat. Sci. Phila., p. 237. 1859.] (Plate XXXVIII, 122.)........*L. imbecilla* O. S.

Body shiny reddish yellow; front yellowish red. [Mon. Dipt. N. Amer., part 4, p. 212. 1869.] (Plate XXXVIII, 123.)........*L. recondita* O. S.

Very large species, wing over 18 mm. (Subgenus *Eutonia* v. d. W.)........23

Smaller species, wing under 15 mm........24

23. Large, wing of female 21.5 mm.; thoracic dorsum reddish brown with three velvety brown stripes, the middle one narrowly split by a line of the ground color; ground color of wings yellowish and brown; basal abdominal tergites yellow without prominent setigerous punctures; cross-vein r close to the tip of R_1. [Proc. Boston Soc. Nat. Hist., vol. 34, p. 126–127, pl. 16, fig. 18. 1909.] (Plate XXXIX, 140.)... *L. alleni* Johns.
Smaller, wing of female 20 mm.; thoracic dorsum gray with three narrow velvety-brown stripes, the middle one split by a broad pale line; ground color of wings hyaline; basal abdominal tergites gray with prominent setigerous punctures; cross-vein r more distant from the tip of R_1. [Journ. N. Y. Ent. Soc., vol. 24, p. 118–120, pl. 8, fig. 2. 1916.] (Plate XXXIX, 141.)................................ *L. marchandi* Alex.
24. R_{2+3} very elongated, nearly twice the length of R_2 alone; cross-vein r on R_{2+3}. [Proc. Acad. Nat. Sci. Phila., p. 238, pl. 4, fig. 26. 1859.] (Plate XXXVIII, 127.) *L. ultima* O. S.
(*L. ultima* is included in both sections of couplet 12 because the character of the position of the cross-vein r is slightly variable and there is a possibility of misinterpretation.)
R_{2+3} shorter, not longer than R_2 alone; cross-vein r on R_2........................25
25. Basal deflection of Cu_1 at the inner end of cell *1st* M_2. (Subgenus *Dactylolabis* O. S.)..26
Basal deflection of Cu_1 near the middle of cell *1st* M_2............................27
26. Wings spotted with brown. [Proc. Acad. Nat. Sci. Phila., p. 240, pl. 3, figs. 28, 28a. 1859.] (Plate XL, 148.).................................... *L. montana* O. S.
Wings unspotted. [Mon. Dipt. N. Amer., part 4, p. 229. 1869.] (Plate XL, 147.) *L. cubitalis* O. S.
27. Wings spotted with brown or distinctly seamed along the cross-veins and deflections of veins...28
Wings clear, or with only the stigmal spot (in *L. poetica* with a tiny cloud at the origin of *Rs* and the basal deflection of R_{4+5})....................................35
28. Wings heavily irrorate with brown over the entire surface. [Proc. Boston Soc. Nat. Hist., vol. 34, p. 127–128, pl. 16, fig. 17. 1909.] (Plate XXXIX, 133.)....*L. irrorata* Johns.
Wings not heavily irrorate over the entire surface, the markings appearing as broad seams to the veins or as dark tips to the wings..............................29
29. R_{2+3} short or very short, much less than R_2 alone; cross-vein r at about midlength of R_2; petiole of cell M_1 longer than or subequal to this cell; brown seams to the veins more extensive; antennae of male short...................................30
R_{2+3} very long, subequal to R_2 alone; cross-vein r just beyond the fork of R_{2+3}; petiole of cell M_1 distinctly shorter than this cell; brown seams on the wings limited to *r-m* and the deflection of R_{4+5}; antennae of male elongated. [Mon. Dipt. N. Amer., part 4, p. 205. 1869.] (Plate XXXVIII, 114.)...................... *L. unica* O. S.
30. Radial sector short, arcuated to almost square at its origin; cross-vein r situated at about midlength of vein R_2, which is oblique; outer end of cell R_2 very broad due to the oblique nature of vein R_2; species with the cross-veins seamed with brown have the tip of the wings more or less infuscated. (Subgenus *Phylidorea* Bigot.)........31
Radial sector longer; vein R_2 not oblique and the cell R_2 not strikingly broadened at its apex; broad grayish brown seams to the cross-veins, deflections of veins, and along *Cu*, but the wing apex only slightly darkened if at all..........................33
31. Coloration of the body yellowish or reddish, the thoracic notum light yellow. [Proc. Acad. Nat. Sci. Phila., p. 235. 1859.] (Plate XXXIX, 128.)........ *L. adusta* O. S.
Coloration of the body dark brown to almost black, the thoracic notum concolorous...32
32. Legs yellow with the brown apices to the segments narrow; costal cell of the wing yellow. [Psyche, vol. 18, p. 195–196, pl. 16, figs. 4, 8. 1911.] (Plate XXXIX, 129.) *L. similis* Alex.
Legs with the femora brown, only a little brightened basally; costal cell of the wings brown. [Journ. N. Y. Ent. Soc., vol. 24, p. 123, pl. 8, fig. 7. 1916.] (Plate XXXIX, 130.).. *L. terrae-novae* Alex.

33. Large species, wing of male over 9 mm.; male with the pleural appendage of the hypopygium pectinated. (Subgenus *Prionolabis* O. S.)........................34
Smaller species, wing of male under 8.5 mm.; male with the pleural appendage of the hypopygium not pectinated, rather sharply pointed. [Journ. N. Y. Ent. Soc., vol. 24, p. 121–122, pl. 8, fig. 5. 1916.] (Plate XL, 146.)................*L. terebrans* Alex.
34. Large, wing of male about 13 mm.; costal and subcostal cells of the wings rich yellow; stigma dark brown; bases of femora bright yellow; anterior apical appendage of male hypopygium bifurcate. [Proc. Acad. Nat. Sci. Phila., p. 239, pl. 4, figs. 27, 27a, 27b. 1859.] (Plate XL, 142.)..*L. rufibasis* O. S.
Smaller, wing of male about 11.5 mm.; wings uniform light yellowish gray; stigma rather indistinct, grayish; bases of femora brownish yellow; anterior apical appendage of male hypopygium simple. [Psyche, vol. 18, p. 198–199, pl. 16, fig. 10. 1911.] (Plate XL, 143.)..*L. simplex* Alex.
35. *Rs* elongated and spurred at its origin; antennae of male elongated. [Mon. Dipt. N. Amer., part 4, p. 207. 1869.] (Plate XXXVIII, 116.)............*L. poetica* O. S.
Rs usually shorter, if elongated not spurred at origin; antennae of male short except in *L. laricicola*...36
36. R_{2+3} elongated, more or less arcuated, longer than the basal deflection of Cu_1........37
R_{2+3} not conspicuously arcuated, short, little if any longer than the basal deflection of Cu_1...38
37. *Rs* and R_{2+3} strongly arcuated; cell *1st* M_2 very broad; antennae of male short. [Proc. Acad. Nat. Sci. Phila., p. 236. 1859.] (Plate XXXVIII, 126.).....*L. toxoneura* O. S.
Rs almost straight; R_{2+3} feebly arcuated but elongate; cell *1st* M_2 narrow; antennae of male elongated. [Psyche, vol. 19, p. 167, pl. 13, fig. 4. 1912.] (Plate XXXVIII, 120.)..*L. laricicola* Alex.
38. Coloration gray; wings with the base strongly yellow, this including *Sc* for its entire length; hind legs with the apical third of femora dark brown, fore femora with the apical two-thirds dark brown; *Rs* rather elongate and somewhat angulated at its origin. [*Phylidorea subcostata* Alex. Can. Ent., vol. 43, p. 288–289. 1911.] (Plate XL, 149.)...*L. subcostata* (Alex.)
Coloration not gray; wings with the base not strongly yellow; legs with the femora yellow, the tips narrowly brown...39
39. Coloration yellowish brown; tuberculate pits distinct; *Rs* nearly straight; antennae of male moniliform. [Mon. Dipt. N. Amer., part 4, p. 220. 1869.]......*L. fratria* O. S.
Coloration yellow to reddish yellow; tuberculate pits not evident; *Rs* short, strongly arcuated; antennae of male not moniliform. (Subgenus *Phylidorea* Bigot.)........40
40. Large species, wing of male 9.5 mm.; abdomen of male without a black subterminal annulus. [Journ. N. Y. Ent. Soc., vol. 8, p. 191. 1900.] (Plate XXXIX, 132.) *L. lutea* Doane
Smaller species, wing of male less than 7.5 mm.; abdomen of male with a black subterminal annulus. [Proc. Acad. Nat. Sci. Phila., p. 594, pl. 25, fig. 4. 1914.] (Plate XXXIX, 131.)..*L. novae-angliae* Alex.
41. Cell R_2 of the wings broadly sessile. [Proc. Acad. Nat. Sci. Phila., p. 597, pl. 27, fig. 28. 1914.] . (Plate XL, 151.)....................................*L. emmelina* Alex.
Cell R_2 of the wings petiolate...42
42. Bases of cells R_3 and *1st* M_2 conspicuously nearer the wing root than cell R_5; petiole of cell R_2 less than half the length of vein R_2; vein R_2 not short, oblique; veins issuing from cell *1st* M_2 about twice the length of the cell.............................43
Bases of cells R_3, R_5, and *1st* M_2 about on a level; petiole of cell R_2 more than half the length of vein R_2; vein R_2 short, oblique; veins issuing from cell *1st* M_2 about equal to or a little longer than the cell, if longer (as in *L. edwardi*) not twice this length....44
43. Prescutal stripes not well-defined; tuberculate pits present; *r* far removed from the tip of R_1; basal deflection of Cu_1 usually at from one-third to one-half the length of the cell *1st* M_2. (Subgenus *Pseudolimnophila* Alex.) [Psyche, vol. 18, p. 196–198, pl. 16, fig. 3. 1911.] (Plate XL, 150.).....................*L. noveboracensis* Alex.

Prescutal stripes dark brown; tuberculate pits lacking; r at the tip of R_1; basal deflection of Cu_1 usually at or close to the fork of M_1. [Proc. Acad. Nat. Sci. Phila., p. 534–535, pl. 27, fig. 46. 1916.] (Plate XL, 157.) . . . . *L. sylvia* Alex.

44. Rs short, about equal to vein R_2 of the wings. [Proc. Acad. Nat. Sci. Phila., p. 241. 1859.] (Plate XL, 152.) . . . . *L. lenta* O. S.

Rs elongate, equal to about twice the length of vein R_2 of the wings 45

45. Mesonotum and pleura yellowish or brownish yellow; wings pale yellow. [Proc. Acad. Nat. Sci. Phila., p. 595–596, pl. 25, fig. 5. 1914.] (Plate XL, 155.) *L. stanwoodae* Alex.

Mesonotum and pleura not yellow 46

46. Pleura and mesonotum clear bluish black with a gray bloom, only the coxae conspicuously light yellow; wings with a yellowish tinge; cross-vein r beyond the fork of R_{2+3} on R_2. [Proc. Acad. Nat. Sci. Phila., p. 241. 1859.] (Plate XL, 153.) . . . . . . *L. quadrata* O. S.

Pleura and mesonotum not so colored; cross-vein r at or before the fork of R_{2+3} 47

47. Pleura of thorax with a conspicuous black dorsal stripe; mesonotum rich brown; wings with a brown suffusion; antennae of male short. [Proc. Acad. Nat. Sci. Phila., p. 596, pl. 25, fig. 6. 1914.] (Plate XL, 154.) . . . . *L. osborni* Alex.

Pleura of thorax without a black dorsal stripe; mesonotum dull yellowish with three confluent dark brown stripes; wings without a distinct dark brown suffusion; antennae of male elongated. [Proc. Acad. Nat. Sci. Phila., p. 533–534, pl. 27, fig. 45. 1916.] (Plate XL, 156) . . . . *L. edwardi* Alex.

Tribe **Hexatomini**

The genera of the tribe Hexatomini may be separated in accordance with the following key:

1. Cell *1st* M_2 open; but one free branch of the media reaching the wing margin; cell R_2 tiny . . . . *Hexatoma* Latr. (p. 920)

Cell *1st* M_2 closed; two or three free branches of the media reaching the wing margin; cell R_2 larger, more elongate 2

2. Feet (in the local species) white; stigma small; cell M_1 present. *Penthoptera* Schin. (p. 921)

Feet not white; stigma large; cell M_1 present or absent . . . . *Eriocera* Macq. (p. 921)

Genus **Hexatoma** Latreille

1809 *Hexatoma* Latr. Gen. Crust. et Ins., vol. 4, p. 260.
1818 *Anisomera* Meig. Syst. Beschr., vol. 1, p. 210.
1818 *Nematocera* Meig. Syst. Beschr., vol. 1, p. 209.
1836 *Peronecera* Curt. Brit. Ent., p. 589.

The small genus Hexatoma includes seventeen described species, about all of which are European. They are mostly small species, with a reduced medial venation that is at first sight difficult to interpret; the manner in which this genus has been evolved from Eriocera is well shown in some of the plastic species of the latter genus, notably *E. austera* Doane, in which all gradations in venation between Eriocera and Hexatoma may be found in a small series. From species such as these it is seen that the elimination of the posterior branch of the media is brought about by

fusion rather than by atrophy. The larvae are carnivorous, and live in wet sand and gravel along the margins of streams (Alexander, 1915 a: 141–148).

Hexatoma megacera (O. S.)

1859 *Anisomera megacera* O. S. Proc. Acad. Nat. Sci. Phila., p. 242.
1909 *Hexatoma megacera* Johns. Proc. Boston Soc. Nat. Hist., vol. 34, p. 126.

Hexatoma megacera is a small, blackish gray fly, the mesonotum having three darker stripes and the male antennae being somewhat elongated and filiform. The characteristic venation is shown in Plate XXXVII, 112.

Genus **Penthoptera** Schiner

1863 *Penthoptera* Schin. Wien. Ent. Monatschr., vol. 7, p. 220.

In the genus Penthoptera there are seven species — four from Europe, two from tropical America, and one local species. The immature stages are spent in rich organic earth, a very different habitat from that of the larvae of the related genera Eriocera and Hexatoma. The larva is carnivorous (Alexander, 1915 a:152–157). In the native species, *Penthoptera albitarsis*, the feet are pure snowy white, which makes the insect a conspicuous one.

Penthoptera albitarsis O. S.

1869 *Penthoptera albitarsis* O. S. Mon. Dipt. N. Amer., part 4, p. 257.

Penthoptera albitarsis is a brownish fly, with the thorax bluish gray, the wings slightly tinged with dusky, and the feet pure snowy white. The flies occur in cool, shady situations and are often very common. In the South (North Carolina) they are frequent in gum swamps. The venation is shown in Plate XXXVII, 104.

Genus **Eriocera** Macquart

1830 *Caloptera* Guer. Voyage de la Coquille, Zool., Ins., pl. 20, fig. 2.
1838 *Eriocera* Macq. Dipt. Exot., vol. 1, p. 74.
1838 *Evanioptera* Guer. Voyage de la Coquille, Zool., vol. 2, p. 287.
1848 *Pterocosmus* Walk. List Dipt. Brit. Mus., vol. 1, p. 78.
1850 *Allarithmia* Loew. Bernstein und Bernsteinfauna, p. 38.
1857 *Oligomera* Dolesch. Natuurk. Tijdschr. Nederl. Indie, vol. 14, p. 387.
1859 *Arrhenica* O. S. Proc. Acad. Nat. Sci. Phila., p. 242.
1859 *Physecrania* Bigot. Ann. Soc. Ent. France, ser. 3, vol. 7, p. 123.
1912 *Androclosma* Enderlein. Zool. Jahrb., vol. 32, part 1, p. 34.
1916 *Globericera* Matsumura. Thous. Ins. Japan, add. 2, p. 471.

Eriocera is one of the larger genera of crane-flies, including about one hundred described species which are most numerous in the tropics of both hemispheres. The larvae are carnivorous. They live in streams, and pupate in sand or gravel (Alexander and Lloyd, 1914). The habits of the common local species *E. longicornis* have been described by the author in another paper (Alexander, 1915 a:149–152). The following key divides the local species of Eriocera:

1. Cell M_1 present 2
   Cell M_1 lacking 3
2. Antennae of male greatly elongated, more than twice the length of the whole body; wings grayish brown; vertical tubercle prominent, brownish on the sides. [*Arrhenica spinosa* O. S. Proc. Acad. Nat. Sci. Phila., p. 244, pl. 4, fig. 30. 1859.] (Plate XXXVII, 105.) *E. spinosa* (O. S.)
   Antennae short in both sexes, extending about to the wing root or a little beyond; wings darker brown; vertical tubercle low, grayish. [Bul. U. S. Geol. Survey, vol. 3, p. 205. 1877.] (Plate XXXVII, 106.) .... *E. brachycera* O. S.
3. Color of body yellow or yellowish red 4
   Color of body brown, gray, or black 5
4. Antennae of male elongated, longer than the body; a blackish spot on the scutal lobes above the wing root. [Mon. Dipt. N. Amer., part 4, p. 255. 1869.] (Plate XXXVII, 109.) .... *E. wilsonii* O. S.
   (*E. antennaria* Doane [Journ. N. Y. Ent. Soc., vol. 8, p. 194, pl. 8, fig. 12, 1900] is the same as *E. wilsonii* O. S.)
   Antennae short in both sexes; no blackish spot on the scutal lobes above the wing root. [Journ. N. Y. Ent. Soc., vol. 8, p. 194, pl. 8, fig. 13. 1900.] .... *E. aurata* Doane
5. Thoracic dorsum gray; antennae of male elongated 6
   Thoracic dorsum brown or black; antennae short in both sexes 7
6. Vertical tubercle of male very large and high, greater than length of eye; first segment of antennal scape uniformly dark; prescutal stripes broad, dark brown, the median stripes about confluent and continued cephalad to the pronotum; cell *1st* M_2 of wings short, pentagonal, usually with a spur into cell R; valves of ovipositor short, blunt, sub-fleshy. [*Anisomera longicornis* Walk., List Dipt. Brit. Mus., vol. 1, p. 82. 1848.] (Plate XXXVII, 107.) .... *E. longicornis* (Walk.)
   (*E. gibbosa* Doane [Journ. N. Y. Ent. Soc., vol. 8, p. 193, pl. 8, fig. 10, 1900] is a doubtful species; in its coloration and, especially, in its venation, it is strikingly like *E. longicornis* [Walk.], but there is no mention in the original description of the size of the antennae.)
   Vertical tubercle of male moderate in size, not so high as length of eye; first segment of antennal scape pale beneath; prescutal stripes narrow, pale brown, the two middle stripes separate, becoming obliterated at about the level of the tuberculate pits; cell *1st* M_2 of wings long, hexagonal; valves of ovipositor elongated, pointed, chitinized. [Psyche, vol. 19, p. 169–170, pl. 13, fig. 9. 1912.] (Plate XXXVII, 108.) .. *E. cinerea* Alex.
7. Cell R_2 short, cross-vein r inserted on R_{2+3}. [Psyche, vol. 19, p. 168–169, pl. 13, fig. 7. 1912.] (Plate XXXVII, 111.) .... *E. fultonensis* Alex.
   Cell R_2 deep, cross-vein r inserted on R_2 8
8. Wings brown, the stigma small, rounded, brown; abdominal tergites brown. [Proc. Acad. Nat. Sci. Phila., p. 243, pl. 3, fig. 31. 1859.] .... *E. fuliginosa* O. S.
   Wings blackish brown, the stigma oval, dark brown; abdominal tergites black. [Proc. Acad. Nat. Sci. Phila., p. 602. 1914.] (Plate XXXVII, 110.) .... *E. tristis* Alex.

Eriocera longicornis, *E. cinerea*, and *E. spinosa* are on the wing in late April and May, the last-named species flying in July. *E. brachycera*, *E. fultonensis*, *E. fuliginosa*, and *E. tristis* are on the wing during the summer months.

Tribe **Pediciini**

The genera of the tribe Pediciini may be separated in accordance with the following key:

1. Antennae with 16 segments 2
   Antennae with 13 or 15 segments 3
2. Cord oblique; cell *1st* M_2 very short, pentagonal; size large, wing over 20 mm.; palpi elongated . . . . *Pedicia* Latr. (p. 923)
   Cord transverse; cell *1st* M_2 elongate; size smaller, wing under 18 mm.; palpi short. *Tricyphona* Zett. (p. 924)
3. A supernumerary cross-vein in cell R_1 . . . . *Dicranota* Zett. (p. 925)
   No supernumerary cross-vein in cell R_1. (Genus *Rhaphidolabis* O. S.) 4
4. Cell M_1 absent . . . . Subgenus *Plectromyia* O. S. (p. 925)
   Cell M_1 present 5
5. Antennae 15-segmented; cell *1st* M_2 closed . . . . Subgenus *Rhaphidolabina* Alex. (p. 925)
   Antennae 13-segmented; cell *1st* M_2 open . . . . Subgenus *Rhaphidolabis* O. S. (p. 925)

The recent accession of several curious new venational types in this tribe indicates that the vein herein held to be the radial cross-vein is in reality the upward deflection of R_2, which, in most species, is short and transverse or but slightly oblique and is fused distally with R_1. A detailed account of this venational peculiarity may be consulted elsewhere (Alexander, 1918 d).

Genus **Pedicia** Latreille

1809 *Pedicia* Latr. Gen. Crust. et Ins., vol. 4, p. 255.
1916 *Daimiotipula* Matsumura. Thous. Ins. Japan, add. 2, p. 463.

Pedicia is a small genus including six species, four of which are North American. The species are among the largest of the Limnobiinae, and with their conspicuous brown-and-white wings attract considerable attention. The larvae are carnivorous, living beneath moss in percolating water and in cold springs (Needham, 1903 b: 285–286). There are two regional species, both of which were originally described from Nova Scotia by Walker. The following key divides the local species of Pedicia:

Wings with the costal margin brown; vein Cu_2 seamed with dark brown. [List Dipt. Brit. Mus., vol. 1, p. 37. 1848.] (Plate XLII, 175.) . . . . *P. albivitta* Walk.
Wings with the costal margin brownish yellow; no brown seam on vein Cu_2. [List Dipt. Brit. Mus., vol. 1, p. 38. 1848.] (Plate XLII, 176.) . . . . *P. contermina* Walk.

Genus **Tricyphona** Zetterstedt

1838 *Tricyphona* Zett. Ins. Lapponica, Dipt., p. 851.
1856 *Amalopis* Hal. Ins. Brit., Dipt., vol. 3, add., p. xv.
1860 *Crunobia* Kol. Wien. Ent. Monatschr., vol. 4, p. 393.
1869 *Amalopis* O. S. Mon. Dipt. N. Amer., part 4, p. 260.

There are about forty known species in the genus Tricyphona. Almost all of these are Holarctic in their distribution, but two occur in the Australasian region. The carnivorous larvae live in moist earth. The following key divides the local species:

1. Cell M with a supernumerary cross-vein; wings heavily clouded and marbled with gray. [*Amalopis hyperborea* O. S. Proc. Acad. Nat. Sci. Phila., p. 292. 1861.] (Plate XLII, 182.) .... *T. hyperborea* (O. S.)
   Cell M without a supernumerary cross-vein; wings with the markings sparse, confined to the region of the veins 2
2. Cell R_2 short-petiolate; costal margin of wings infuscated. [*Amalopis inconstans* O. S. Proc. Acad. Nat. Sci. Phila., p. 247, pl. 3, fig. 32. 1859.] (Plate XLII, 177.) *T. inconstans* (O. S.)
   Cell R_2 sessile; costal margin of wings not infuscated 3
3. Wings subhyaline or hyaline, unspotted 4
   Wings spotted or marked with darker 5
4. Stigma of wings brown; male hypopygium conspicuously hairy; wings of female sub-atrophied. [Can. Ent., vol. 49, p. 30–31. 1917.] (Plate XLII, 179, 180.) *T. autumnalis* Alex
   Stigma of wings pale; male hypopygium small, not conspicuously hairy; wings of female normally developed. [*Amalopis calcar* O. S. Proc. Acad. Nat. Sci. Phila., p. 247 1859.] (Plate XLII, 178.) .... *T. calcar* (O. S.)
5. Fusion of Cu_1 with M_3 extensive, subequal to the part of M_3 before the cross-vein *m* [*Amalopis auripennis* O. S. Proc. Acad. Nat. Sci. Phila., p. 247. 1859.] (Plate XLII, 181.) .... *T. auripennis* (O. S.)
   Fusion of Cu_1 with M_3 transient if present at all, usually less than one-half of the part of M_3 before the cross-vein *m* 6
6. Coloration of body light brown; *m-cu* obliterated by the fusion of Cu_1 on M_3. [Proc. Acad. Nat. Sci. Phila., p. 598–599, plate, fig. 1914.] (Plate XLII, 183.) *T. katahdin* Alex
   Coloration of body gray; *m-cu* present ....
7. Scape of antenna yellowish or brownish yellow, the flagellum much darker, brown abdominal tergites brown, the margins of the segments pale producing a banded appearance; wings with large rounded clouds at the tips of the longitudinal veins and along the cross-veins. [*Amalopis vernalis* O. S. Proc. Acad. Nat. Sci. Phila., p. 291. 1861 (Plate XLII, 185.) .... *T. vernalis* (O. S.
   Scape of antenna dark brown, concolorous with the flagellum; abdominal tergites brown unbanded; wings with the pattern almost obsolete, reduced to tiny dots and seams [Proc. Acad. Nat. Sci. Phila., p. 538–540 pl. 28, fig. 53. 1916.] (Plate XLII, 184 *T. paludicola* Alex

In the local fauna, *T. vernalis* and *T. paludicola* are early spring species *T. auripennis* and *T. calcar* late spring species, and *T. katahdin* and *T. autumnalis* late summer species.

Genus **Dicranota** Zetterstedt

1838 *Dicranota* Zett. Ins. Lapponica, Dipt., p. 851.

In the genus Dicranota there are about fifteen known species, restricted to the northern Holarctic region. The species are readily distinguished from those of Rhaphidolabis by the supernumerary cross-vein in cell R_1 of the wings. The larvae are carnivorous, feeding largely on Tubifex worms (Miall, 1893). The local species of Dicranota may be separated according to the following key, which is adapted from a key to the North American species already published by the author (Alexander, 1914 b:601).

1. Cell M_1 absent 2
   Cell M_1 present 3
2. Halteres with the knobs darkened; antennae of male much longer than the thorax. [Mon. Dipt. N. Amer., part 4, p. 281–282. 1869.] .... *D. eucera* O. S.
   Halteres pale; antennae of male short. [Proc. Acad. Nat. Sci. Phila., p. 249. 1859.] (Plate XLI, 169.) .... *D. rivularis* O. S.
3. Cell *1st* M_2 present; color of body yellowish. [Proc. Acad. Nat. Sci. Phila., p. 599–600, pl. 27, fig. 31. 1914.] (Plate XLI, 167.) .... *D. pallida* Alex.
   Cell *1st* M_2 absent; color of body gray. [Proc. Acad. Nat. Sci. Phila., p. 600. 1914.] (Plate XLI, 168.) .... *D. noveboracensis* Alex.

Genus **Rhaphidolabis** Osten Sacken

1869 *Rhaphidolabis* O. S. Mon. Dipt. N. Amer., part 4, p. 284.
1869 *Plectromyia* O. S. Mon. Dipt. N. Amer., part 4, p. 282.

The genus Rhaphidolabis includes about fourteen described species found in the Holarctic region and in the mountainous sections of the Oriental region. The larvae are carnivorous, and live in rich organic mud or in the streams near by. Needham (1908:212–214) has given a description of the larva of the species *R. tenuipes*. The following key, adapted from a key to the North American species of Rhaphidolabis already published by the author (Alexander, 1916:541–542), divides the local species of the genus:

1. Antennae 15-segmented; cross-vein *m* present. (Subgenus *Rhaphidolabina* Alex.) [Mon. Dipt. N. Amer., part 4, p. 288. 1869.] (Plate XLI, 170.) .... *R. flaveola* O. S.
   Antennae 13-segmented; cross-vein *m* absent 2
2. Cell M_1 absent. (Subgenus *Plectromyia* O. S.) [*Plectromyia modesta* O. S. Mon. Dipt. N. Amer., p. 284. 1869.] (Plate XLI, 174.) .... *R. modesta* (O. S.)
   Cell M_1 present. (Subgenus *Rhaphidolabis* O. S.) 3
3. Cell R_2 petiolate. [Mon. Dipt. N. Amer., p. 287. 1869.] (Plate XLI, 171.) *R. tenuipes* O. S.
   Cell R_2 sessile 4

4. Coloration grayish brown, the prescutum with three dark brown stripes; abdomen dark brown with paler caudal margins to the segments; wings very pale brown, the radial sector very short, arcuated, angulated, or spurred. [Proc. Acad. Nat. Sci. Phila., p. 543–544, pl. 28, fig. 57. 1916.] (Plate XLI, 173.) .... *R. cayuga* Alex.
   Coloration reddish brown, the prescutum with three indistinct stripes; abdomen yellowish brown, the hypopygium bright yellow; wings nearly hyaline, the radial sector somewhat elongated, slightly arcuated. [Proc. Acad. Nat. Sci. Phila., p. 544–545, pl. 28, fig. 58. 1916.] (Plate XLI, 172.) .... *R. rubescens* Alex.

SUBFAMILY **Cylindrotominae**

The genera of the subfamily Cylindrotominae may be separated in accordance with the following key:

1. Head and intervals of the prescutum with numerous deep punctures. *Triogma* Schin. (p. 926)
   Head and intervals of the prescutum smooth 2
2. Three branches of the radius reaching the wing margin. *Phalacrocera* Schin. (species *neoxena* Alex.) (p. 927)
   Two branches of the radius reaching the wing margin, caused by an apparent fusion of R_{1+2+3} 3
3. Three branches of the media reaching the wing margin .... *Cylindrotoma* Macq. (p. 927)
   Two branches of the media reaching the wing margin 4
4. Cross-vein *r-m* present; cross-vein *m* obliterated by the fusion of M_3 on M_{1+2}; antennae of male tipuline in structure .... *Phalacrocera* Schin. (species *tipulina* O. S.) (p. 927)
   Cross-vein *r-m* usually obliterated by the fusion of R_{4+5} on M_{1+2}; cross-vein *m* present; antennae of male subpectinate, the individual flagellar segments almost cordate. *Liogma* O. S. (p. 927)

Genus **Triogma** Schiner

1863 *Triogma* Schin. Wien. Ent. Monatschr., vol. 7, p. 223.

There are but two known species of Triogma, one occurring in Europe and the other in northeastern North America. The larval life of the European species, the only one that is known, is spent on aquatic mosses growing in mountain torrents. The insects closely resemble the species of Liogma in all their stages.

Triogma exculpta O. S.

1865 *Triogma exculpta* O. S. Proc. Ent. Soc. Phila., vol. 4, p. 239.

Triogma exculpta is a rather small, dull brown fly, with the wings suffused with brown. The head and the sides of the thorax are deeply punctured. The fly is rare and is insufficiently known. The venation is very much like that in the genus Liogma. (Johnson, 1909:131.)

Genus **Phalacrocera** Schiner

1863 *Phalacrocera* Schin. Wien. Ent. Monatschr., vol. 7, p. 224.

The small genus Phalacrocera includes but three described species — two North American and one European. They are of especial interest because of certain venational features which they possess and which aid materially in explaining the remarkable venation of the more specialized species of Cylindrotominae (p. 863). The larva is aquatic, living on submerged plants. It is greenish brown in color, and the body is provided with numerous long, flexible filaments which are quite unlike the spiny armature of the more specialized members of the subfamily. The species are northern in their distribution and are most frequently found in bogs and boggy meadows. The local species may be separated by the following key:

Vein R_2 present and persistent to the wing margin; wings dark brown. [Proc. Acad. Nat. Sci. Phila., p. 603–605, pl. 25, fig. 10. 1914.] (Plate XXX, 9.) ... *P. neoxena* Alex.
Vein R_2 lost by atrophy; wings grayish brown. [Proc. Ent. Soc. Phila., vol. 4, p. 241. 1865.] (Plate XXX, 8.) .... *P. tipulina* O. S.

Genus **Cylindrotoma** Macquart

1834 *Cylindrotoma* Macq. Suit. à Buff., vol. 1, Hist. Nat. Ins., Dipt., p. 107.

The genus Cylindrotoma forms a small group of crane-flies, including two European and three North American species. They are all similar in color, being usually bright yellow with black stripes on the thorax, in this respect suggesting some species of Nephrotoma. The larvae live on the lower side of the leaves of various monocotyledonous and dicotyledonous plants such as Allium, Anemone, Trautvetteria, Stellaria, and Viola, the insect feeding on the leaf tissue. The larvae are green in color and are usually provided with fleshy points and processes.

The following key divides the local species of Cylindrotoma:

Tarsi dark brown. [Proc. Ent. Soc. Phila., vol. 4, p. 236. 1865.] (Plate XXX, 6.) *C. americana* O. S.
Tarsi yellow. [*C. tarsalis* Johns., Psyche, vol. 19, p. 2, fig. 4, 1912. *C. anomala* Johns., Psyche, vol. 19, p. 2–3, fig. 3, 1912.] (Plate XXX, 7.) .... *C. tarsalis* Johns.

Genus **Liogma** Osten Sacken

1869 *Liogma* O. S. Mon. Dipt. N. Amer., part 4, p. 298.

In the genus Liogma there are three described species, all occurring in the North Temperate Zone. The coloration of the adult flies is

sordidly yellow and black, with the surface shiny. The antennae of the male are submoniliform with the segments heart-shaped, as shown in figure 125, I (page 850). The larva, which has been discussed by the writer in another paper (Alexander, 1914 a), lives in certain terrestrial mosses (as Hypnum). It is bright green in color, with darker stripes on the sides, and closely simulates the appearance of its host plant, the illusion being heightened by the spines and excrescences that cover the body.

Liogma nodicornis (O. S.)

1865 *Triogma nodicornis* O. S. Proc. Ent. Soc. Phila., vol. 4, p. 239.
1887 *Liogma nodicornis* O. S. Berl. Ent. Ztschr., vol. 31, p. 226.

Liogma nodicornis is a common fly in Canadian conditions thruout North America. In color it is mainly yellow, the head black and shiny, the thorax yellow with three more or less confluent shiny black stripes on the dorsum, the pleura with one or two large black blotches. The venation (Plate XXX, 5) is somewhat variable, especially in the fusion of R_{4+5} on M_{1+2}, these being in some cases broadly fused (as shown in figure 128, I, page 862), in other cases with the cross-vein *r-m* apparent.

SUBFAMILY **Tipulinae**

Tribe **Dolichopezini**

The genera of the tribe Dolichopezini may be separated in accordance with the following key:

1. Tip of vein R_2 atrophied; *Rs* very short, transverse, simulating a cross-vein; second anal vein long, about two-thirds the length of the first; *Sc* moderate in length, ending in *R*. 2
   Tip of vein R_2 present, the vein almost perpendicular to R_{2+3} at its origin; *Rs* long, strongly arcuated at its origin; second anal vein very short, about one-third the length of the first; *Sc* very long, ending in costa. . . . . *Brachypremna* O. S. (p. 928)
2. Cell *1st* M_2 lacking; basal deflection of Cu_1 in a long fusion with *M*, breaking away before the fork of *M*. . . . . *Dolichopeza* Curt. (p. 929)
   Cell *1st* M_2 present; basal deflection of Cu_1 in punctiform contact with M_{3+4} beyond the fork of *M*. . . . . *Oropeza* Needm. (p. 929)

Genus **Brachypremna** Osten Sacken

1886 *Brachypremna* O. S. Berl. Ent. Ztschr., vol. 30, p. 161.

The genus Brachypremna includes but seven described species, all of which are tropical American. A single species, *B. dispellens*, ranges

into the southern limits of the territory here considered. This is a curious fly which is common all over the South, where in some sections it is called "weaver." The flies of this species have a remarkable dance over a vertical height of several feet, and have been aptly termed "the kings of the dancing crane-flies." The larval life is spent in decaying wood.

Brachypremna dispellens (Walk.)

1860 *Tipula dispellens* Walk. Trans. Ent. Soc. Lond., n. ser., vol. 5, p. 334.
1886 *Brachypremna dispellens* O. S. Berl. Ent. Ztschr., vol. 30, p. 162.

Brachypremna dispellens is a large, brownish fly. The pleura is silvery white with narrow brown stripes. The legs are very long, and the tibiae and tarsi are pale yellowish white. The venation is shown in Plate XLIII, 188.

Genus **Dolichopeza** Curtis

1825 *Dolichopeza* Curt. Brit. Ent., p. 62.
1830 *Leptina* Meig. Syst. Beschr., vol. 6, pl. 65, fig. 10.
1846 *Apeilesis* Macq. Dipt. Exot., Suppl. 1, p. 8.

The genus Dolichopeza includes about eighteen described species, only one of which occurs in the New World. The immature stages are spent in or beneath moist mosses.

Dolichopeza americana Needm.

1908 *Dolichopeza americana* Needm. 23d Rept. N. Y. State Ent., p. 211, pl. 16, fig. 5.

Dolichopeza americana is a curious fly usually found beneath bridges and culverts, or in similar darkened situations. The adults hang suspended from the roof by the anterior two pairs of feet, the wings being spread wide apart and the long, white-tipped hind legs dangling conspicuously. The dark color of the body and the pure white tarsi easily serve to distinguish the species from the forms of Oropeza that may be found with it. The wing venation is shown in Plate XLIII, 187.

Genus **Oropeza** Needham

1908 *Oropeza* Needm. 23d Rept. N. Y. State Ent., p. 211.

In the genus Oropeza there are seven described species, all occurring within the limits of this paper. While they are closely related to one another, most of them are apparently valid species. They occur in the

same type of situations as does the preceding species — beneath bridges, culverts, in crannies of cliffs, on the inclined sides of boulders along mountain streams, and in similar places. Their position when at rest is very different from that of *Dolichopeza americana*, as they hang from the roof by the front pair of feet only, the other legs dangling and the wings being folded over the abdomen. In this last-named feature they differ conspicuously from the often-associated Dolichopeza. The immature stages are spent in moist earth, or (in the case of *O. obscura*) in a dry moss, *Hedwigia albicans*, where they were first discovered by Hyslop. The larvae are sluggish and of a rather dark green color. The following key is adapted from one given by Johnson (1909:117–118):

1. Tarsi, at least, entirely white....................2
   Tarsi yellow or brownish....................3
2. Digitiform appendages of male genitalia short or rudimentary; ventral margin deeply and narrowly emarginate. [Proc. Boston Soc. Nat. Hist., vol. 34, p. 121, pl. 15, fig. 12. 1909.]....................*O. albipes* Johns.
   Digitiform appendages of male genitalia moderate in length; ventral margin broadly emarginate. [Proc. Boston Soc. Nat. Hist., vol. 34, p. 121–122, pl. 15, figs. 5, 11. 1909.]....................*O. subalbipes* Johns.
3. Halteres with the knobs dark brown....................4
   Halteres entirely yellow....................7
4. Stripes of thorax distinct; ventral margin deeply emarginate....................5
   Stripes of thorax obscure; ventral margin but slightly emarginate....................6
5. Pleura yellow, unspotted. [Proc. Boston Soc. Nat. Hist., vol. 34, p. 119–120, pl. 15, fig. 6. 1909.]....................*O. dorsalis* Johns.
   Pleura yellow, spotted. [Proc. Boston Soc. Nat. Hist., vol. 34, p. 120, pl. 15, fig. 9. 1909.]....................*O. venosa* Johns.
6. Thorax opaque. [Proc. Boston Soc. Nat. Hist., vol. 34, p. 122, pl. 15, figs. 7, 10. 1909.] (Plate XLIII, 186.)....................*O. obscura* Johns.
   Thorax shining. [Proc. Boston Soc. Nat. Hist., vol. 34, p. 122–123, pl. 15, fig. 8. 1909.]....................*O. obscura polita* Johns.
7. Ventral margin of male genitalia deeply and narrowly emarginate. [Proc. Boston Soc. Nat. Hist., vol. 34, p. 118–119, pl. 15, figs. 2, 3, 1909. New name for *Tipula annulata* Say, Journ. Acad. Nat. Sci. Phila., vol. 3, p. 25 (1823), preoccupied.] *O. sayi* Johns.
   Ventral margin broadly emarginate. [Proc. Boston Soc. Nat. Hist., vol. 34, p. 119, pl. 15, fig. 4. 1909.]....................*O. similis* Johns.

Tribe **Ctenophorini**

The following key separates the two genera of the tribe Ctenophorini:

Antennae of male with three pectinations on the flagellar segments, each segment with a single pectination on the apical half in addition to the usual basal pair; ovipositor of female greatly elongated, saber-like....................*Tanyptera* Latr. (p. 931)

Antennae of male with two pairs of pectinations on the flagellar segments, one pair being subbasal and the other subapical; ovipositor of female short and of the normal tipuline structure....................*Ctenophora* Meig. (p. 931)

Genus **Tanyptera** Latreille

1805 *Tanyptera* Latr. Hist. Nat. Crust. et Ins., vol. 14, p. 286.
1832 *Xiphura* Brulle. Ann. Soc. Ent. France, vol. 1, p. 206.

In the genus Tanyptera there are supposedly twelve described species, of which three or four are from eastern North America and the remainder are from the Palaearctic region. The remarkable variation in color, however, is strongly indicative that the number of species is very much less than that given, and it is possible that there is but a single species within the limits of this paper. The question can be definitely settled only by the wholesale breeding of larvae to the adult stage. Until more is known about these flies it is best to recognize the full number of forms, always keeping in mind, however, the foregoing remarks.

The larvae live in the wood of deciduous trees, often in prostrate trunks that are fairly sound. The adult flies are easily distinguished from all other crane-flies by the tripectinate antennal segments of the male and the elongated acicular ovipositor in the female. The flies are shiny, and often are brilliantly colored with black and reddish yellow, simulating Ichneumonidae and other hymenopterous insects.

The following key divides the local species of Tanyptera:

1. Wings smoky black; body coloration black, the male with feet and abdomen also black, the female with legs and base of abdomen reddish yellow. [*Ctenophora fumipennis* O. S. Proc. Ent. Soc. Phila., vol. 3, p. 47. 1864.] . . . . *T. fumipennis* (O. S.)
   Wings not black 2
2. Wings tinged with topazine yellow, the stigma dark brown; body coloration varying from black to yellow, the feet reddish yellow. [*Ctenophora topazina* O. S. Proc. Ent. Soc. Phila., vol. 3, p. 47–48. 1864.] . . . . *T. topazina* (O. S.)
   Wings hyaline, the stigma brown; head black; body coloration varying from black to yellow. [*Ctenophora frontalis* O. S. Proc. Ent. Soc. Phila., vol. 3, p. 48–49. 1864.] (Plate XLIII, 191.) . . . . *T. frontalis* (O. S.)

Genus **Ctenophora** Meigen.

1800 *Flabellifera* Meig. Nouv. Class. Mouch., p. 13 (*nomen nudum*).
1803 *Ctenophora* Meig. Illiger's Mag., vol. 2, p. 263.
1910 *Phoroctenia* Coq. Proc. U. S. Nat. Mus., vol. 37, p. 589.

In the genus Ctenophora a condition exists which is similar to that in Tanyptera, there being fifteen described species which are very closely related and many of which are undoubtedly synonymous. Two forms are here recognized, and even these may represent but one species. A number of larvae of Ctenophora were found in a decaying tree by Johannsen (1910), who reared from them a considerable number of adults

which showed well the dimorphic nature of the flies of this group. Some of the specimens of each sex were entirely black, while others were reddish yellow with the wings tipped with darker. Specimens having hyaline wings are often taken.

The larvae live in decaying wood. The adult flies are easily distinguished by the double bipectinate antennae of the male (fig. 125, M, page 850), and the serrate antennae and relatively short ovipositor in the female.

The local species of the genus may be separated by the following key:

Wings with the entire apex beyond the cord tinged with blackish; thorax yellowish brown with darker spots. [Proc. Ent. Soc. Phila., vol. 3, p. 45–46. 1864.] (Plate XLIII, 189, normal form; 190, black form, the wing not shaded in this drawing.)...... *C. apicata* O. S.

Wings nearly hyaline, with a large brown cloud between the cord and the wing tip but not reaching the apex; thorax yellow with a wedge-shaped median brown stripe. [Proc. Ent. Soc. Phila., vol. 3, p. 46. 1864.]............................... *C. nubecula* O. S.

Tribe **Tipulini**

The genera of the tribe Tipulini may be separated in accordance with the following key:

1. Flagellar segments of antennae not verticillate................. *Stygeropis* Loew (p. 932)
   Flagellar segments of antennae verticillate...2
2. Abdomen greatly elongated in both sexes, much longer than the wing alone; the male hypopygium simple in structure, the ninth sternite very long with the pleurites lying in this concavity...3
   Abdomen not greatly elongated in the male sex, rarely so in the female sex (*Tipula longiventris*), not longer than the wing; the male hypopygium more complicated in structure, if simple the ninth sternite not shaped as described above................4
3. Cell M_1 sessile; wings strongly suffused with reddish brown... *Aeshnasoma* Johns. (p. 933)
   Cell M_1 petiolate, long-petiolate in *Longurio minimus*, short-petiolate in *L. testaceus*; wings grayish, the subcostal cell brown........................ *Longurio* Loew (p. 933)
4. *Rs* usually very short, almost transverse, simulating a cross-vein; cell M_1 sessile or short-petiolate; basal deflection of Cu_1 or the *m-cu* cross-vein joining *M* at or before its fork; coloration usually yellow and black, shiny...5
   Rs usually longer, not simulating a cross-vein; cell M_1 always petiolate; basal deflection of Cu_1 or the *m-cu* cross-vein joining *M* at its fork or underneath the middle of cell *1st* M_2; coloration usually dull brown, yellow, or gray. (Genus *Tipula* Linn.).......6
5. Cells of wings glabrous.................................. *Nephrotoma* Meig. (p. 934)
   Apical cells of wings pubescent.................... Subgenus *Odontotipula* Alex. (p. 943)
6. Cells of wings glabrous.............................. Subgenus *Tipula* Linn. (p. 942)
   Apical cells of wings pubescent...7
7. Apical cells of wings with an abundant short pubescence; body coloration dull brown, as in species of Oropeza....................... Subgenus *Trichotipula* Alex. (p. 942)
   Apical cells of wings with a sparse short pubescence; thoracic dorsum dark-colored with paler stripes................................ Subgenus *Cinctotipula* Alex. (p. 943)

Genus **Stygeropis** Loew

1844 *Prionocera* Loew. Stett. Ent. Ztg., vol. 5, p. 170; preoccupied.
1863 *Stygeropis* Loew. Berl. Ent. Ztschr., vol. 7, p. 298.

The genus Stygeropis includes about ten species, all confined to the temperate and arctic regions. The species of Stygeropis are readily distinguished from those of Tipula by the lack of verticils on the antennae (fig. 125, N, page 850). The immature stages are spent in rich organic mud. The pupae have a peculiar character in their elongate unequal breathing horns.

Stygeropis fuscipennis Loew

1865 *Stygeropis fuscipennis* Loew. Berl. Ent. Ztschr., vol. 9, p. 129.

Stygeropis fuscipennis is a medium-sized fly, with the thorax grayish brown, the pleura clearer gray, the abdomen brownish yellow, and the wings strongly tinged with brown. The wing venation is shown in Plate XLIII, 194, the ninth tergite of the male hypopygium in Plate XLIX, 255. These singular flies are characteristic inhabitants of marshy (helophytic) situations, and appear on the wing in July and August.

Genus **Aeshnasoma** Johnson

1909 *Aeshnasoma* Johns. Proc. Boston Soc. Nat. Hist., vol. 34, p. 115–116.

Aeshnasoma is a monotypic genus which is close to Longurio but probably separable from it. The fly is known only from the type station, New Jersey, where it is apparently not uncommon. Larvae were found in a cold stream near Riverton, New Jersey, by Johnson. They were not reared, but the striking resemblance to the larva of Longurio leaves no doubt as to their identity.

Aeshnasoma rivertonensis Johns.

1909 *Aeshnasoma rivertonensis* Johns. Proc. Boston Soc. Nat. Hist., vol. 34, p. 116, pl. 16, figs. 13–15.

Aeshnasoma rivertonensis is a large fly, nearly resembling *Longurio testaceus* but with the body coloration strongly reddish brown, including the wings, and with cell M_1 sessile. The abdomen of the male is 30 mm. in length, the wing 22 mm. The ninth tergite of the male hypopygium is shown in Plate XLIX, 257.

Genus **Longurio** Loew

1869 *Longurio* Loew. Berl. Ent. Ztschr., vol. 13, p. 3.

The small genus Longurio includes about six described species from widely separated areas of the earth, two being from eastern North America. It is probable that the species recently described by Edwards from Formosa is not a Longurio, as its hypopygium is very different from the peculiar type characteristic of this group (Plate LIII, 329). The immature stages are spent in sand or gravel near running water, usually in mountainous conditions. The bulky, semi-transparent larvae of *L. testaceus* are probably the largest crane-fly larvae to be found in eastern America; the writer is indebted to Mr. Hyslop for specimens which, altho not bred, can scarcely belong to any other species. The pupae are remarkable in their elongate breathing horns, these being nearly 20 mm. in length. The adult fly of *L. testaceus* is the largest crane-fly in eastern America, in the female sex even excelling the better-known *Holorusia grandis* of the West. It is found in cool, shaded woods, near streams, and is very wary and difficult to capture, usually alighting in the midst of a pile of brush or similar débris from which it cannot be swept with a net.

The following key divides the local species of Longurio:

Large, wing of male about 25 mm., abdomen 36 mm.; cell M_1 with its petiole very short [Berl. Ent. Ztschr., vol. 13, p. 3. 1869.] (Plate XLIII, 192, wing; Plate XLIX, 256, ninth tergite; Plate LIII, 329, lateral aspect of male hypopygium.).........*L. testaceus* Loew

Small, wing of male about 15 mm., abdomen 18 mm.; cell M_1 with its petiole elongated. [Proc. Acad. Nat. Sci. Phila., p. 605–606, pl. 27, fig. 32. 1914.] (Plate XLIII, 193.) *L. minimus* Alex.

Genus **Nephrotoma** Meigen

1800 *Pales* Meig. Nouv. Class. Mouch. p. 14 (*nomen nudum*).
1803 *Nephrotoma* Meig. Illiger's Mag., p. 262.
1834 *Pachyrrhina* Macq. Suit. à Buff., vol. 1, Hist. Nat. Ins., Dipt., p. 88.

The large genus Nephrotoma includes about one hundred and twenty-five species of medium-sized flies, which present a great uniformity of size and color but a considerable diversity in the structure of the male antennae. In many instances the species run close to those of Tipula, and the two genera are undoubtedly very close together. The writer (Alexander, 1915 b:466) has removed about six of the North American species of Nephrotoma from this genus and placed them in Tipula. As a rule the species of Nephrotoma are brilliantly colored with red, yellow, orange, or black, the body being shiny; in *N. macrocera* and to a lesser extent in the *tenuis* group, however, the body is dull. In the genus Tipula the colors are brown, gray, and yellow, and are dull, the only shiny species

being the ones that have been removed from Nephrotoma and referred to Tipula on other characters. The immature stages of the known species are spent in moist earth and in decaying wood.

The local species of Nephrotoma may be separated in accordance with the following key:

1. Thoracic stripes black or largely black 2
   Thoracic stripes, if present, brownish or reddish 8
2. Prescutum with the anterior lateral angles of the lateral stripes and the ends of the V-shaped suture deep velvety black; pleura with faint reddish markings. [*Pachyrrhina virescens* Loew. Berl. Ent. Ztschr., vol. 8, p. 62. 1864.] . . . . . *N. virescens* (Loew)
   Prescutum with the stripes uniform black thruout 3
3. Wings with the ground color hyaline 4
   Wings strongly tinged with brown or dusky, at least basally 6
4. Lateral stripes on prescutum curved laterad at their anterior ends. [*Pachyrrhina incurva* Loew. Berl. Ent. Ztschr., vol. 7, p. 293. 1863.] (Plate XLIV, 204.) *N. incurva* (Loew)
   Lateral stripes on prescutum straight 5
5. A small black spot on the vertex between the antennal bases; wings tipped with brown; abdominal segments banded with black. [*Pachyrrhina pedunculata* Loew. Berl. Ent. Ztschr., vol. 7, p. 293. 1863.] (Plate XLIV, 203.) . . . . . *N. pedunculata* (Loew)
   No small black spot between the antennal bases; wings not tipped with darker; abdominal segments trivittate, the lateral stripes interrupted, the median stripe continuous. [*Pachyrrhina vittula* Loew. Berl. Ent. Ztschr., vol. 8, p. 63. 1864.] *N. vittula* (Loew)
6. Lateral stripes on prescutum curved laterad at their anterior ends. [*Tipula lineata* Scop. Ent. Carniol., p. 320. 1763.] . . . . . *N. lineata* (Scop.)
   Lateral stripes on prescutum straight 7
7. Prescutum with the ground color orange-yellow; scutellum and pleura mostly black; abdomen with black dorsal spots. [*Pachyrrhina lugens* Loew. Berl. Ent. Ztschr., vol. 8, p. 63. 1864.] (Plate XLIV, 202.) . . . . . *N. lugens* (Loew)
   Prescutum with the ground color obscure yellow; scutellum and pleura mostly yellow; abdomen with a black dorso-median stripe. [Proc. Acad. Nat. Sci. Phila., p. 467–468, pl. 16, fig. 1. 1915.] (Plate XLIV, 205.) . . . . . *N. penumbra* Alex.
8. Thoracic dorsum dull, opaque; antennae of male very elongated, the flagellum black. [*Tipula macrocera* Say. Journ. Acad. Nat. Sci. Phila., vol. 3, p. 24. 1823.] (Plate XLIV, 200.) . . . . . *N. macrocera* (Say)
   Thoracic dorsum more or less shiny; if at all opaque, the antennae of both sexes very short 9
9. Antennal segments uniform in color 10
   Antennal segments bicolorous 17
10. A velvety black spot at the anterior end of the lateral prescutal stripe. [*Pachyrrhina punctum* Loew. Berl. Ent. Ztschr., vol. 7, p. 294. 1863.] . . . . . *N. punctum* (Loew)
    No velvety black spot at the anterior end of the lateral prescutal stripe 11
11. Occiput opaque with a shining triangular spot in the middle 12
    Occiput shining 14
12. A black spot at each end of the V-shaped suture. [*Tipula ferruginea* Fabr. Syst. Antl., p. 28. 1805.] (Plate XLIV, 198.) . . . . . *N. ferruginea* (Fabr.)
    No black spots at the ends of the V-shaped suture 13
13. Stigma pale, brownish yellow. [*Pachyrrhina occipitalis* Loew. Berl. Ent. Ztschr., vol. 8, p. 65. 1864.] . . . . . *N. occipitalis* (Loew)
    Stigma dark, blackish brown. [*Pachyrrhina gracilicornis* Loew. Berl. Ent. Ztschr., vol. 8, p. 66. 1864.] . . . . . *N. gracilicornis* (Loew)

14. Head with a shining triangular spot. [*Pachyrrhina occipitalis* Loew. Berl. Ent. Ztschr., vol. 8, p. 65. 1864.] . . . . *N. occipitalis* (Loew)
Head unicolorous 15
15. Wings strongly tinged with brown, especially along the costal region. [*Pachyrrhina okefenoke* Alex. Wash. Univ. Studies, p. 97–98. 1915.] . . . . *N. okefenoke* (Alex.)
Wings not strongly brown along the costal region 16
16. Head and thorax yellowish, almost opaque; color in life strongly greenish. [*Pachyrrhina tenuis* Loew. Berl. Ent. Ztschr., vol. 7, p. 297. 1863.] (Plate XLIV, 199.) *N. tenuis* (Loew)
Head orange except the lateral margins of the vertex; thorax shining. [*Pachyrrhina sodalis* Loew. Berl. Ent. Ztschr., vol. 8, p. 64. 1864.] . . . . *N. sodalis* (Loew)
17. Segments of flagellum black at the base 18
Segments of flagellum yellow at the base 20
18. Wings strongly tinged with yellow; occiput without a clear, shining triangle. [*Pachyrrhina xanthostigma* Loew. Berl. Ent. Ztschr., vol. 8, p. 65. 1864.] (Plate XLIV, 201.) . . . . *N. xanthostigma* (Loew)
Wings not strongly tinged with yellow; occiput with a clear, shining triangle 19
19. Costal region hyaline; stigma dark brown. [*Pachyrrhina abbreviata* Loew. Berl. Ent. Ztschr., vol. 7, p. 295. 1863.] . . . . *N. abbreviata* (Loew)
Costal region darker; stigma yellowish brown. [*Pachyrrhina suturalis* Loew. Berl. Ent. Ztschr., vol. 7, p. 295. 1863.] . . . . *N. suturalis* (Loew)
20. Antennae with 13 segments. [*Pachyrhina breviorcornis* Doane. Ent. News, vol. 19, p. 178–179. 1908.] . . . . *N. breviorcornis* (Doane)
Antennae with more than 13 segments 21
21. Stigma yellowish brown; wing apex not darker; antennae of male 19-segmented. [*Pachyrrhina eucera* Loew. Berl. Ent. Ztschr., vol. 7, p. 296. 1863.] . . . . . . *N. eucera* (Loew)
Stigma dark brown; wing apex distinctly darkened; antennae of male 16-segmented. [*Pachyrrhina polymera* Loew. Berl. Ent. Ztschr., vol. 7, p. 297. 1863.] *N. polymera* (Loew)

After the above key was completed, Dietz (1918) published an extensive revision of the American species of the genus. A number of his new species are found within the faunal limits of this paper. The more salient characters of the regional species are here briefly summarized, and these species should be considered in addition to the key.

Nephrotoma perdita (Dietz). (Pages 116–117 of reference cited.)

Yellow; mouth parts and palpi yellow; occiput with a shiny brown pentagon; thoracic stripes black, narrowly margined with rusty, the lateral stripes curved outward and ending in an opaque black spot; wings grayish subhyaline, stigma brownish black. Wing of female, 14.5 mm. (Manitoba, August.)

N. hirsutula (Dietz). (Pages 118–119 of reference.)

Very closely resembling *N. macrocera*, but with the wings sparsely pubescent. Eighth sternite of male deeply emarginate behind and with a digitiform lobe from the base of the notch. Wing of male, 12.5 mm. (Pennsylvania, May.)

N. urocera (Dietz). (Pages 119–120 of reference.)
N. cornifera (Dietz). (Pages 120–121 of reference.)

These two species are close to *N. okefenoke* but are easily separated by the male genitalia. They are from Virginia and North Carolina.

N. calinota (Dietz). (Pages 121–122 of reference.)

Yellow; antennal flagellum bicolorous; frontal prolongation of head dark brown medially; occiput opaque with a brown line; thoracic stripes silvery gray pruinose, the lateral stripes

outcurved and ending in a velvety black spot; wings grayish subhyaline, more yellowish basally, costal region brownish yellow. Wing of male, 11 mm. (Michigan and Maryland, June and July.)

N. opacivitta (Dietz). (Page 123 of reference.)

Similar to *N. calinota*, but with the antennae stout, the flagellum beyond the first segment blackish, the segments deeply incised beneath. Mesonotal prescutum with a median velvety black stripe; wings broad, tinged with brown; abdomen with a broad dark brown lateral stripe. Wing of male, 12 mm. (Manitoba.)

N. evasa (Dietz). (Pages 124–125 of reference.)

Yellow; antennae entirely yellowish; occiput with a shiny, broadly triangular spot; prescutum with an anterior median black mark; abdominal tergites margined posteriorly with yellowish brown. Wing of female, 13.5 mm. (Michigan, July.)

N. festina (Dietz). (Pages 126–127 of reference.)

Pale yellow; antennae very slender, the flagellar segments yellow, the outer ones more yellowish brown; occiput shiny; wings tinged with yellowish, the costal area pale yellow, the stigma brown; abdomen on either side with a row of black dashes. Wing of male, 12.5 mm. (Pennsylvania and Maryland, July and August.)

N. temeraria (Dietz). (Page 128 of reference.)

Yellow; antennae entirely yellowish; occiput opaque with a narrow shiny brown line; wings faintly tinged with grayish yellow, the costal area and along the veins more yellowish, the stigma brown; abdomen with a broad, pale brown, dorsal stripe, and with a row of black dashes along each lateral margin of the tergum. Wing of female, 13 mm. (Michigan, July.)

N. cingulata (Dietz). (Pages 131–133 of reference.)

Close to *N. xanthostigma*. Antennae of male elongated, the flagellar segments bicolorous, dark brown at base; thoracic dorsum highly polished, testaceous, the stripes poorly defined; wings strongly tinged with yellow as in *N. xanthostigma*, the costal region and along vein *Cu* more saturated, the stigma pale brown. Wing of male, 11 mm. (Pennsylvania, July and August.)

N. obliterata (Dietz). (Pages 133–134 of reference.)

Close to *N. xanthostigma*. Flagellar segments of antennae bicolorous, the segments dusky, blackish at base; occiput shiny; thorax sulfur yellow, the stripes rusty, the transverse suture black medially; wings grayish subhyaline, stigma yellowish; abdomen with a dark brown dorsal stripe and lateral rows of spots. Wing of male, 12.5 mm. (Ottawa, Michigan, and Pennsylvania, July and August.)

N. wyalusingensis (Dietz). (Pages 134–135 of reference.)

Close to *N. obliterata*. Head dark testaceous; flagellar segments of antennae bicolorous, yellowish brown, black at base; occiput shiny, a small brown spot at base; prescutum shiny yellow, the stripes dark rusty; wings pale brown, the costal region yellowish; abdomen dark testaceous, the lateral margins of tergites and the posterior margins of segments bordered with black. Wing of male, 12.5 mm. (Pennsylvania, August.)

N. approximata (Dietz). (Pages 136–137 of reference.)

Closely resembling *N. cingulata*, but with the flagellar segments brown, rusty at base. Antennae of male long, slender; occiput shiny with a dark brown stripe; thoracic stripes rusty brown; wings grayish, stigma brownish yellow; abdomen with black lateral stripes, the segments margined posteriorly with brown. Wing of male, 12 mm. (Pennsylvania, August.)

N. stigmatica (Dietz). (Pages 137–138 of reference.)

Close to *N. breviorcornis*. Honey yellow; antennae of male short, the flagellar segments bicolorous, segments brown, yellow at base; thoracic stripes dark rusty; wings yellowish subhyaline, the costal area and along *Cu* more saturated, the stigma dark; abdomen with a brown dorsal stripe and more or less complete lateral stripes, a mid-ventral row of small black spots on the sternites. Wing of male, 12.5 mm. (Pennsylvania, August.)

Genus **Tipula** Linnaeus

1758 *Tipula* Linn. Syst. Natur., vol. 10, p. 585.
1864 *Anomaloptera* Lioy. Atti dell' Institut Veneto, ser. 3, vol. 9, p. 218.
1887 *Oreomyza* Pokorny. Wien. Ent. Ztg., vol. 6, p. 50.

Tipula is the largest genus of crane-flies. It includes some six hundred and fifty described species, found in most parts of the world and very abundant on most of the continental areas but rare or lacking on many of the smaller oceanic islands. Obviously such a group of very closely related species presents considerable difficulty in classification. The keys to the species of any region are so cumbersome as to be almost unworkable, and yet it is very difficult to lessen this problem. In the present paper the geographical area has been considerably restricted and the number of included species is thus reduced. It is further reduced by the omission of species that have not been definitely recognized since their original characterization, thus eliminating species described by Walker, Macquart, and others; the inclusion of these species in keys is altogether guesswork, and it is far better to omit them until their types can be examined and the determination made final. The species described by Say, Doane, and Loew are fairly well known and very few of these are in doubt.

In order to supplement the keys, practically all the species are figured. In those forms having a characteristic wing pattern, it is the wing that is shown; while in those that evince notable characters of the male hypopygium, various parts of this organ are figured. In this genus, as in many others, it is almost impossible to separate the females unless they have been taken in copulation with the males.

The life histories of species in th s genus are diverse, ranging from strictly aquatic forms to those occurring in wet mud, in moist soil, and in decaying wood.

An attempt is herein made to divide the local species into groups, the following characters being considered in making this division:

Color characters, as in the *collaris* group, in which the body coloration is strikingly like that in Nephrotoma, and the dimorphic groups (*T. fuliginosa*, *T. annulicornis*), with light-colored males and brown or black females.

Antennae, whether longer in the male than in the female, or short in both sexes.

Wings: pubescence in the apical cells, as in the subgenera Trichotipula, Cinctotipula, and Odontotipula; the features of wing venation, such as the atrophy of the tip of vein R_2; the retention of the *m-cu* cross-vein and its position in regard to the fork of M; the shape of the cell *1st* M_2; the wing pattern, which divides the species into three groups, as follows:

striatae, wings streaked longitudinally;
marmoratae, wings cross-banded or spotted in various ways;
subunicolores, wings hyaline or unicolorous.

Male hypopygium, whether the sclerites of the ninth segment are separate, or the tergite is fused with the sternite, or all the sclerites are fused into a continuous ring. The primitive character is to have a separate tergite, pleurite, and sternite, and specialization in the organ is shown by the fusion of these parts. The pleurite is first lost, by fusing with the sternite, but a part of the pleural suture is retained in all except the most specialized forms. The culmination of the organ in this genus is the fusion of the tergite with the already fused sterno-pleurite so as to form a continuous ring. The eighth sternite shows many curious modifications, which have already been discussed (p. 873).

Female hypopygium, which is much more homogeneous than the male hypopygium but which still shows many peculiar modifications and tendencies. There may be a sudden narrowing of the organ, as in *T. besselsi*, or the valves may be shortened and fleshy, and feebly chitinized, as in the *collaris* and *bicornis* groups. The most striking modification apparently is that seen in the *arctica* group, in which the ovipositor has two valves lying transversely and with the outer margins variously serrated.

Four subgenera are included in the genus, classified as follows:

A. Subgenus *Trichotipula* Alex.— Apical cells of the wings with abundant short hairs; coloration dull, as in Oropeza, but vein R_2 persistent for its entire length.

Tipula (*Trichotipula*) *oropezoides* Johns.

B. Subgenus *Cinctotipula* Alex.— Apical cells of the wings with a sparse, short pubescence; coloration dark brown, the mesonotum with pale stripes; ninth tergite with the caudal margin concave; antennae of the male elongated.

Tipula (*Cinctotipula*) *algonquin* Alex.
Tipula (*Cinctotipula*) *unimaculata* (Loew)
Tipula (*Cinctotipula*) *dorsolineata* Doane

C. Subgenus *Odontotipula* Alex.— Apical cells of the wings with a very sparse, short pubescence, most evident in cell R_5; coloration bright shiny yellow and red, as in species of Nephrotoma; antennae of the male short.

Tipula (*Odontotipula*) *unifasciata* (Loew)

D. Subgenus *Tipula* Linn.— No pubescence in the apical cells of the wings. This subgenus is divided into twenty-two groups, as follows:

1. The *collaris* group.— Coloration shiny black and yellow, as in species of Nephrotoma; wings with the *m-cu* cross-vein beneath the middle of cell *1st* M_2; female ovipositor with the valves short and fleshy.

Tipula collaris Say
T. nobilis (Loew)

2. The *pachyrhinoides* group.— Similar to the preceding in coloration; wings with the *m-cu* cross-vein nearer to the fork of M than to the medial cross-vein; female ovipositor with the valves elongate and chitinized.

T. pachyrhinoides Alex.

3. The *bicornis* group.— Nasus very short to indistinct; coloration dull yellow to brownish yellow, with the thoracic stripes usually distinct; venation with cell *1st* M_2 very small and pentagonal; male hypopygium with the ninth tergite usually tumid; female ovipositor with the valves short, blunt, subfleshy.

T. bicornis Forbes
T. megaura Doane
T. morrisoni Alex.
T. parshleyi Alex.
T. johnsoniana Alex.

4. The *valida* group.— A heterogeneous collection of subgroups, as follows:

a. The *valida* subgroup.— Very large species; the eighth sternite with prominent lateral lobes and a depressed median lobe.

T. valida Loew
T. hirsuta Doane

b. The *umbrosa* subgroup.— Large species; the eighth sternite provided with conspicuous lateral lobes, and the caudal area between with two chitinized points.

T. umbrosa Loew
T. flavoumbrosa Alex.

c. The *australis* subgroup.— Medium-sized species; the lateral lobes of the eighth sternite (*T. australis*) tending to disappear (*T. dietziana*) and pass into the fourth subgroup.

T. australis Doane
T. dietziana Alex.

d. The *submaculata* subgroup.— A great assemblage of forms, including the majority of the *subunicolores*. Wing practically unicolorous (except in *T. huron*) but the obliterative streak well marked; ninth tergite variously notched medially; eighth sternite provided with tufts of short to long hairs, in the specialized forms (*T. tuscarora*) passing into a single powerful bristle on either side.

T. mainensis Alex.
T. mingwe Alex.
T. georgiana Alex.
T. monticola Alex.
T. translucida Doane
T. cincticornis Doane
T. penicillata Alex.
T. triton Alex.
T. submaculata Loew
T. tuscarora Alex.
T. huron Alex.

5. The *besselsi* group.— A small group of high arctic species; coloration blue-gray; head, thorax, and coxae with abundant long white hair; valves of the ovipositor suddenly narrowed, weak.

T. besselsi O. S.
T. piliceps Alex.

6. The *aperta* group.— A reduced species, with the venation in process of atrophy, the medial cross-vein lacking.

T. aperta Alex.

7. The *apicalis* group.— An isolated species that has probably come from the *valida* group; wing broadly tipped with brown; ninth tergite deeply notched medially. This species is possibly closer to *T. mainensis* than this grouping would indicate.

T. apicalis Loew

8. The *hermannia* group.— Wings sparsely blotched with darker; ninth tergite with a prominent, compressed, median lobe; antennae of the male elongate; not dimorphic.

T. hermannia Alex.

9. The *annulicornis* group.— Dimorphic, the males light-colored, the females dark brown, the wings practically unicolorous; male antennae elongate to very elongate (*T. taughannock*); ninth tergite with a conspicuous median lobe and more or less prominent lateral lobes.

T. annulicornis Say
T. taughannock Alex.

10. The *fuliginosa* group.— Dimorphic, the males light-colored (*T. speciosa*), the females very dark brown (*T. fuliginosa*) with white markings; ninth tergite asymmetrical, the right pleurite produced caudad in a prominent two-cleft arm; ninth tergite deeply notched medially.

T. fuliginosa (Say)

11. The *trivittata* group.— Wings conspicuously cross-banded, an uninterrupted white band beyond the cord; ninth tergite notched, with a small tooth at the base of the notch.

T. trivittata Say
T. angulata Loew
T. entomophthorae Alex.

12. The *subfasciata* group.— Wings conspicuously cross-banded, an uninterrupted white band beyond the cord; tip of vein R_2 atrophied. The species of this group are evidently derived from the last preceding group, being reduced forms.

T. subfasciata Loew
T. penobscot Alex.

13. The *hebes* group.— A well-marked group of species, including forms with elongate antennae in the male sex and those with the antennae short in both sexes; hypopygium elongated and curiously upturned at an angle with the remainder of the abdomen; eighth sternite three-lobed, the margins clothed with golden-yellow hairs; wing pattern a peculiar spotting and blotching of browns, grays, and whites.

T. hebes Loew
T. latipennis Loew
T. grata Loew
T. afflicta Dietz
T. helderbergensis Alex.

14. The *macrolabis* group.— Ninth pleurite greatly produced caudad into finger-like lobes; wing pattern spotted, the costal region with four larger blotches.

T. macrolabis Loew
T. macrolaboides Alex.

T. loewiana Alex. may be considered as coming close to this group, the ninth pleurite being produced caudad as a short, subspatulate lobe.

15. The *arctica* group.— A well-defined group of species; female ovipositor with but two functional valves, which are strongly serrated along their outer margins; ninth tergite showing two distinct types, in one of which (*T. arctica, T. alticola*) the sclerite is very small and the caudal margin is evenly concave and heavily chitinized, in the second (*T. longiventris, T. caroliniana*) the tergite is feebly chitinized and the sclerite has a small dorsal transverse knob at about midlength.

T. arctica Curt.
T. labradorica Alex.
T. serrulata Loew
T. septentrionalis Loew
T. longiventris Loew
T. caroliniana Alex.
T. fultonensis Alex.
T. alticola Alex.

16. The *angustipennis* group.— A large group of species; wings spotted with white on a brown or a grayish ground; eighth sternite usually unarmed, but in some species (*T. serta*) with a small median lobe, in others (*T. senega*) with prominent fleshy lateral lobes; ninth tergite variously shaped; outer pleural appendage broad and fleshy; female ovipositor with the valves usually elongated, much shorter and sublyriform in *T. senega*, never serrated.

T. balioptera Loew
T. centralis Loew
T. canadensis Loew
T. ternaria Loew
T. angustipennis Loew
T. ignota Alex.
T. serta Loew
T. senega Alex.

17. The *marmorata* group.— Wing pattern pale, marmorate gray, brown, and hyaline; *m-cu* cross-vein usually distinct and rather close to the fork of *M*.

T. fragilis Loew
T. ignobilis Loew

18. The *abdominalis* group.— An extensive group of large flies, including some of the largest in the genus. The species are more numerous in the West and thence southward (*T. oblique-fasciata, T. craverii, T. commiscibilis, T. abluta, T. rupicola, T. albimacula*, and

others). Wing pattern characteristic, with whitish or hyaline spots at the ends of the veins at the wing margin; ninth tergite tending to be notched, and often rather massive.

T. abdominalis (Say)

19. The *dejecta* group.— Ninth tergite with two lobes on the caudal margin, in *T. iroquois* slender and lying parallel, in *T. dejecta* more divergent; ninth tergite strongly fused with the sternite in *T. dejecta*, the condition found in the remaining groups to be considered.

T. iroquois Alex.
T. dejecta Walk.
T. aprilina Alex.

20. The *tephrocephala* group.— Sclerites of the ninth segment fused into a continuous ring; ninth tergite with two slender parallel lobes on the caudal margin.

T. tephrocephala Loew
T. cayuga Alex.

21. The *tricolor* group.— Species with striate wings. This group is divisible into the following two subgroups, which pass readily into each other:

a. The *tricolor* subgroup.— Wings with a heavy striate pattern.

T. sayi Alex.
T. tricolor Fabr.
T. caloptera Loew
T. bella Loew
T. fraterna Loew
T. strepens Loew
T. eluta Loew
T. conspicua Dietz
T. ludoviciana Alex.
T. sackeniana Alex.
T. vicina Dietz

b. The *perlongipes* subgroup.— Wings subhyaline.

T. perlongipes Johns.
T. sulphurea Doane
T. kennicotti Alex.

The *tricolor* group has the sclerites of the ninth segment fused into a continuous ring; the ninth tergite has a single broad, depressed, median lobe, which in some species is indistinctly cut in two by a median split.

22. The *cunctans* group.— Sclerites of the ninth segment fused into a continuous ring; ninth tergite with a conspicuous median notch.

T. cunctans Say
T. ultima Alex.

The local species of the genus Tipula may be separated in accordance with the following key:

1. Wings with a distinct pubescence in the apical cells. 2
   Wings without pubescence in the apical cells. (Subgenus *Tipula* Linn.). 5
2. Pubescence of wings abundant, including all the apical cells from R_1 to M_4; coloration dull as in species of Oropeza; antennae black, the scape light yellow; thorax brownish gray, the prescutum with three darker brownish gray stripes; basal deflection of Cu_1 and the *m-cu* cross-vein at or near the fork of M; male hypopygium with each caudo-ventral angle of the ninth sternite prolonged caudad into a pale, slender, finger-like lobe. [Proc. Boston Soc. Nat. Hist., vol. 34, no. 5, p. 131. 1909.] (Plate XLIII, 195, wing; Plate XLIX, 258, ninth tergite; Plate LIII, 330, lateral aspect of male hypopygium.) (Subgenus *Trichotipula* Alex.). . . . . *T. oropezoides* Johns.
   Pubescence of wings less abundant, not extending beyond cells R_3, R_5, M_1, and M_2 and confined to the centers of the cells; coloration usually bright as in Nephrotoma, or else the prescutum dark-colored with pale stripes. 3

3. Coloration bright shiny yellow, reddish, and black; vertex shiny, with a black spot along the inner margin of each eye and a linear dark brown median area; thorax yellow with three shiny reddish stripes, the middle one narrowly divided; male antennae very short, not attaining the wing base; pubescence of the wings confined to cell R_5; male hypopygium with the ninth sternite produced caudad in two powerful tooth-like lobes. [*Pachyrrhina unifasciata* Loew. Berl. Ent. Ztschr., vol. 7, p. 294. 1863.] (Plate XLIV, 206, wing; Plate XLIX, 262, ninth tergite.) (Subgenus *Odontotipula* Alex.) . . . . *T. unifasciata* (Loew)

   Coloration dull brown and yellow; vertex opaque without black marks; prescutum dull, dark-colored with paler stripes, the median one at least well indicated; male antennae elongate, reaching about to the base of the abdomen; pubescence of the wings more extensive, from cell R_3 to M_2. (Subgenus *Cinctotipula* Alex.) 4

4. Antennae with the flagellum bicolorous, the basal swelling of each segment black, the elongate pedicel dull yellow; abdomen without distinct crossbands to the segments. [*Pachyrrhina unimaculata* Loew. Berl. Ent. Ztschr., vol. 8, p. 64. 1864.] (Plate XLIII, 196, wing; Plate XLIX, 259, ninth tergite.) . . . . *T. unimaculata* (Loew)

   Antennae with the flagellum unicolorous; abdomen with the caudal half of the segments dark brown, the basal half more yellowish producing a banded appearance. [Proc. Acad. Nat. Sci. Phila., p. 469–471, pl. 16, fig. 2. 1915.] (Plate XLIII, 197, wing; Plate XLIX, 260, ninth tergite; Plate LIII, 324, eighth sternite.) . . *T. algonquin* Alex.

5. Coloration as in Nephrotoma — shiny, contrasting blacks, yellows, and reddish browns . . 6

   Coloration dull brown, gray, or blackish, not at all shiny 8

6. Head with a linear black median mark extending from between the antennal bases to the occiput, sides of the abdomen without patches of light silvery gray; female ovipositor, elongate, pointed, the valves chitinized. [Proc. Acad. Nat. Sci. Phila., p. 471–472. pl. 16, fig. 3. 1915.] (Plate XLIV, 209, wing.) . . . . *T. pachyrhinoides* Alex-

   Head without a black median line; sides of the abdomen with patches of light silvery, gray pruinosity; female ovipositor very blunt, truncate, the valves not chitinized, simulating the hypopygium of the male (*collaris* group) 7

7. Head orange-yellow, the occiput with a grayish black spot; prescutum orange-yellow with three dull gray-black stripes; posterior margin of the postnotum, and the apical half of the first abdominal segment, light gray. [Journ. Acad. Nat. Sci. Phila., vol. 3, p. 25. 1823.] (Plate XLIV, 207, wing.) . . . . *T. collaris* Say

   Head orange-yellow, with a large brownish orange spot on each side of the vertex touching the inner margin of the eye; prescutum shiny, light honey-yellow, with three shiny jet-black or reddish black stripes; posterior margin of the postnotum, and the apical half of the first abdominal segment, not light gray; wings yellowish, the cord and the apex narrowly seamed with brown. (*Pachyrrhina nobilis* Loew. Berl. Ent. Ztschr., vol. 8, p. 62. 1864.] (Plate XLIV, 208, wing; Plate XLIX, 261, ninth tergite.) *T. nobilis* (Loew)

8. Wings striped or streaked longitudinally with brown or reddish brown, this including the costal region and along *Cu*; cell *M* usually hyaline or nearly so; male hypopygium with the sclerites of the ninth segment fused into a continuous ring (*tricolor* group) 9

   Wings not striped nor streaked as above, the costal margin in some cases darkened but if so with no brown seams on the other veins 14

9. Wings with cell R_5 hyaline or nearly so, at least on its apical half, thus being continuous or nearly so with the area in cell *M* 10

   Wings with cell R_5 infuscated, concolorous with cells R_3 and M_1 13

10. Large species, wing of male over 20 mm.; base of cell R_5 darkened 11

    Smaller species, wing of male under 18 mm.; cell R_5 hyaline 12

11. Large, wing of male 25 mm., and darker-colored; prescutal stripes heavily margined with dark brown; antennae short, not attaining the wing base, dark brown thruout; abdominal tergites with a dark brown sublateral stripe; wings with the pattern clear-cut, a bright yellow spot in cell *1st* R_1; cells M_1, M_2, M_4, and Cu_1 infuscated; male

hypopygium with the ninth tergite (Plate XLIX, 267) having a slender median lobe, truncated at the apex, with a conspicuous chitinized claw on either side of the tergal region. [Berl. Ent. Ztschr., vol. 7, p. 292. 1863.] (Plate XLV, 214, wing.) *T. caloptera* Loew

(Two species are apparently confused under this name; true *caloptera* has the bases of cells M_1, M_2, and M_4 pale, as figured, and the male hypopygium lacks the clawlike appendage on either side of the median lobe of the ninth tergite.)

Smaller, wing of male 23 mm. or less, and paler-colored; prescutal stripes not heavily margined with brown; antennae longer, extending nearly to the base of the abdomen, bicolorous; abdominal tergites without a dark brown sublateral stripe; wings without a conspicuous yellow spot in cell *1st* R_1; cells M_1, M_2, M_4, and Cu_1 hyaline basally; male hypopygium with the ninth tergite (Plate XLIX, 264) having a broad median lobe, rounded at the apex; no lateral claws on the tergal region. [Berl. Ent. Ztschr., vol. 7, p. 291. 1863.] (Plate XLV, 215, wing.)........................*T. strepens* Loew

12. Antennae short, with only the basal segments of the flagellum distinctly bicolorous; wing pattern more clear-cut, the costal stripe broader and darker brown, vein Cu and the basal deflection of Cu_1 with a broad dark brown seam. [Berl. Ent. Ztschr., vol. 7, p. 291. 1863.] (Plate XLV, 216, wing; Plate XLIX, 265, ninth tergite.) *T. bella* Loew

Antennae longer, with all except the terminal segments of the flagellum distinctly bicolorous; wing pattern less distinct and rather poorly defined, the brown stripes and seams much paler. [Berl. Ent. Ztschr., vol. 7, p. 290. 1863.] (Plate XLV, 217, wing.)..*T. eluta* Loew

13. White obliterative streak before the wing cord passing beyond cell *1st* M_2 and almost reaching the wing margin; male hypopygium having the region of the ninth tergite without a brush of bristles on its lateral part. [Berl. Ent. Ztschr., vol. 8, p. 56. 1864.] *T. fraterna* Loew

White obliterative streak before the wing cord ending in the extreme base of cell M_4; male hypopygium having the region of the ninth tergite (Plate XLIX, 263) with a brush of long, stiff, reddish bristles on its lateral part. [Ent. Syst., vol. 4, p. 235. 1794.] (Plate XLV, 218, wing.)..*T. tricolor* Fabr.

(*Tipula vitrea* v. d. W. [Tijd. Ent., vol. 24, p. 150, pl. 15, fig. 5, 1881] is very close to *T. tricolor* but may be a good species. The description of *T. vitrea* calls for a testaceous abdomen with a brown lateral stripe, while in *T. tricolor* the abdomen is concolorous thruout.).

14. Costal margin of wings dark brown; male hypopygium with the sclerites of the ninth segment fused into a continuous ring....................................15

Costal margin of wings not dark brown..16

15. Wings with the brown costal margin including the base and the cephalic parts of cells R and R_1; male hypopygium with the ninth tergite (Plate XLIX, 266) having a low, broad, depressed, median protuberance (*tricolor* group). [*T. sayi* Alex., Psyche, vol. 18, p. 194, 1911. *T. costalis* Say, preoccupied, Journ. Acad. Nat. Sci. Phila., vol. 3, p. 23, 1823.] (Plate XLV, 219, wing.)..................................*T. sayi* Alex.

Wings with the brown costal margin including cells C and Sc only; male hypopygium with the ninth tergite (Plate L, 274) having a median notch. [Journ. Acad. Nat. Sci. Phila., vol. 3, p. 23. 1823.] (Plate XLV, 220, wing; Plate LIII, 332, lateral aspect of male hypopygium.)......................................*T. cunctans* Say

16. Wings strongly tinged with yellow; a brownish cloud at the end of vein *2d A*; male hypopygium with the sclerites of the ninth segment fused into a continuous ring and the tergal region (Plate L, 273) notched medially. [*T. ultima* Alex., Insec. Inscit. Menst., vol. 3, p. 128, 1915. *T. flavicans* Fabr., Syst. Antl., p. 24, 1805; written *flavescens*.] (Plate XLVII, 232, wing; the figure of the wing reproduced far too dark to give an idea of the pattern in this species. Plate LIII, 333, lateral aspect of male hypopygium.)..*T. ultima* Alex.

Wings not strongly tinged with yellow, or if so without a brown cloud at the end of vein *2d A*..17

17. Wings spotted, banded, clouded, or tipped with brown or gray....................18
Wings unicolorous — hyaline, yellowish, or dark brown, in many cases, however, with the stigmal spot present; usually with a pale vitreous obliterative streak at or before the cord, extending from before the stigma to the region of cell *1st* M_2 or beyond; in some cases the costal region a little darkened, and perhaps a vitreous spot beyond the stigma in the base of cell R_2..68
18. Tip of vein R_2 atrophied..19
Tip of vein R_2 present, reaching the wing margin................................20
19. Wings long and narrow, in the male 14 mm. long; cell *1st* M_2 elongate, as long as or longer than cell M_1; blotch at the origin of the sector connected with the blotches in cell R. [Berl. Ent. Ztschr., vol. 7, p. 282. 1863.] (Plate XLVIII, 248, wing.) *T. subfasciata* Loew
Wings short and broad, in the male 11.6 mm. long; cell *1st* M_2 short and broad, about two-thirds the length of cell M_1; a small brown spot at the origin of the sector; a dark spot at the base of the wing. [Proc. Acad. Nat. Sci. Phila., p. 472–474, pl. 16, fig. 4. 1915.] (Plate XLVIII, 247, wing; Plate L, 275, ninth tergite; Plate LIII, 334, lateral aspect of male hypopygium.)................................*T. penobscot* Alex.
20. Wings with the apex broadly dark brown, extending from the outer end of cell R_2 to the end of cell M_2; no brown markings proximad of the cord; body coloration yellowish brown; scape of the antennae bright yellow; wing under 15 mm. [Berl. Ent. Ztschr., vol. 7, p. 277. 1863.] (Plate XLVIII, 254, wing; Plate LI, 302, ninth tergite; Plate LIV, 342, lateral aspect of male hypopygium.)..................*T. apicalis* Loew
Wings with the dark markings not confined to the apex, or if the tip is darkened the coloration of the body is gray and the scape of the antenna is dark brown (*T. iroquois*) or the size of the fly is larger (*valida* group, wings over 18 mm.)................21
21. Wings banded brown and white, with a broad, uninterrupted white crossband beyond the stigma, extending from the end of cell *2d* R_1 to the middle of cell M_4, or beyond to the wing margin..22
Wings without an uninterrupted white crossband beyond the stigma................23
22. Smaller species, wing of male less than 15 mm.; antennal flagellum bicolorous; thorax gray with four broad brownish stripes; wings with the white fasciae narrow; male hypopygium with the ninth tergite (Plate LI, 291) narrowly notched medially. [Berl. Ent. Ztschr., vol. 8, p. 61. 1864.] (Plate LIV, 340, lateral aspect of male hypopygium.)..*T. angulata* Loew
Larger, wing of male over 15 mm.; antennal flagellum unicolorous; thorax gray with an interrupted pattern of dots and narrow brown lines; wings with the white fasciae broad, the basal one especially broad; male hypopygium with the ninth tergite (Plate LI, 294) broadly and shallowly notched caudally, bearing a more or less bifurcate median tooth. [Journ. Acad. Nat. Sci. Phila., vol. 3, p. 26. 1823.] (Plate XLVI, 226, wing.)..*T. trivittata* Say
23. Large, length of male over 25 mm.; vertex light yellow; thoracic dorsum with a velvety black pattern margined with paler, producing an ocellate appearance; abdominal tergites bright orange with a broad brownish black stripe on either side; segments 7 to 9 dark brownish black. [*Ctenophora abdominalis* Say. Journ. Acad. Nat. Sci. Phila., vol. 3, p. 18. 1823.] (Plate XLV, 210, wing; Plate LI, 299, ninth tergite.) *T. abdominalis* (Say)
Smaller, length of male under 20 mm.; not colored as above......................24
24. Males (as known)..25
Females (as known)..49
25. Coloration bright orange, the thoracic dorsum without darker stripes; wings yellowish basally, more clouded with brown apically; a small brown spot at the base of the wing and another at the origin of the sector; antennae bicolorous; male hypopygium asymmetrical, the right pleurite produced caudad into a prominent two-cleft arm. [*Ctenophora fuliginosa* Say. Journ. Acad. Nat. Sci. Phila., vol. 3, p. 18. 1823.] (Plate XLVIII, 245, wing of male; Plate LI, 289, ninth tergite.)... *T. fuliginosa* (Say)
Coloration not as above..26

26. Male hypopygium with the ninth tergite (Plate L, 287) produced caudad into a compressed median lobe; antennae elongate, bicolorous; wings with an extensive brownish gray blotch before the cord, occupying the ends of cells R and M and the lower basal angle of cell Cu_1; a broad cloud on the petiole of cell M_1; prescutum light gray, with four broad dark gray stripes. [*T. hermannia* Alex., Proc. Acad. Nat. Sci. Phila., p. 480, 1915. *T. fasciata* Loew, preoccupied, Berl. Ent. Ztschr., vol. 7, p. 279, 1863.] (Plate XLV, 211, wing; Plate LIV, 343, lateral aspect of male hypopygium.) *T. hermannia* Alex.

Male hypopygium not as above 27

27. Wings with a pale gray tinge, more brownish in cell M along vein Cu; hyaline spots in the anal cells, at two-thirds the length of cell M_1, before the stigma, and an interrupted band before the cord extending to cell *1st* M_2; body coloration gray, the prescutum with four dark brown stripes; male hypopygium small, not conspicuously elongated or enlarged (*marmorata* group) 28

Wings brown or dark gray, with a pattern of white or hyaline spots and blotches 29

28. Stripes on the prescutum ending at the level of the pseudosutural foveae, the median pair blunt at their anterior ends; apical tergites of the abdomen not conspicuously darkened. [Berl. Ent. Ztschr., vol. 7, p. 279. 1863.] (Plate XLVIII, 250, wing; the figure is much darker than in normal specimens. Plate LI, 297, ninth tergite.) *T. fragilis* Loew

Median stripes of the prescutum extending about to the anterior margin of the sclerite, deeply bifid at the anterior end; apical segments of the abdomen largely blackish. [Berl. Ent. Ztschr., vol. 7, p. 280. 1863.] (Plate LI, 298, ninth tergite.) *T. ignobilis* Loew

29. Male hypopygium with the ninth segment elongate-cylindrical, strongly upturned; eighth sternite with the caudal margin tripartite and clothed with yellow hairs; wings with a variegated brown, gray, and white pattern (*hebes* group) 30

Male hypopygium with the ninth segment not strongly upturned 33

30. Antennae elongated in the male, extending about to the base of the abdomen 31

Antennae short in both sexes, extending about to the wing root 32

31. Antennal flagellum bicolorous; bladelike processes of the male hypopygium not elongated nor spiraliform. [Berl. Ent. Ztschr., vol. 7, p. 285. 1863.] (Plate XLVIII, 249, wing.) .... *T. hebes* Loew

Antennal flagellum uniform dark brown, at least apically; bladelike processes of the male hypopygium elongate, spiraliform. [Berl. Ent. Ztschr., vol. 8, p. 60. 1864.] (Plate LI, 293, ninth tergite.) .... *T. latipennis* Loew

(*T. ottawaensis* Dietz is the same as *T. latipennis* Loew.)

32. Antennal flagellum yellowish brown; appendiculate process of the male hypopygium slender and pointed apically. [Berl. Ent. Ztschr., vol. 7, p. 281. 1863.] (Plate LI, 292, ninth tergite.) .... *T. grata* Loew

Antennal flagellum dark brown; appendiculate process of the male hypopygium broad, obtusely pointed at the apex. [*T. afflicta* Dietz, Trans. Amer. Ent. Soc., vol. 40, p. 351–352, pl. 13, figs. 5, 6, pl. 14, fig. 2, 1914, as *T. suspecta* Dietz.] .. *T. afflicta* Dietz

(*T. afflicta* Dietz is close to *T. grata* Loew but apparently separable from it.)

33. Wing with four large brown subequidistant blotches along the radial vein, the second at the origin of the sector, the fourth on vein R_3; male hypopygium with the ninth pleurite greatly produced into slender, chitinized, digitiform processes (*macrolabis* group) 34

Wings variously marked but without four large brown subequidistant blotches along the radial vein; male hypopygium with the ninth pleurite not greatly produced 35

34. Ninth tergite (Plate LI, 295) rather squarely truncated across the caudal margin, with a sharp median tooth; apex of the ninth pleurite ending in acute teeth (Plate LIII, 322). Northeastern North America. [Berl. Ent. Ztschr., vol. 8, p. 58. 1864.] (Plate XLVII, 233, wing; the brown blotches along R do not show clearly in the figure.) .... *T. macrolabis* Loew

Ninth tergite (Plate LI, 296) not square across the caudal margin; the sharp median tooth subtended on either side by a flattened divergent lobe; apex of the ninth pleurite rounded and blunt, not toothed (Plate LIII, 323). Western North America. [Can. Ent., vol. 50, p. 69–70. 1918.] . . . . *T. macrolaboides* Alex.

35. Wings with the apex narrowly and irregularly darkened; narrow brown seams along the cord; antennae dark brown thruout; prescutum gray, with darker gray stripes which are narrowly margined with dark brown; pleura clear light gray; male hypopygium with the ninth tergite large (Plate LI, 300), the caudal margin produced into two short, parallel lobes, one on either side of the median line. [*T. iroquois* Alex., Insec. Inscit. Menst., vol. 3, p. 128, 1915. *T. cincta* Loew, preoccupied, Berl. Ent. Ztschr., vol. 7, p. 288, 1863.] (Plate XLVIII, 252, wing; Plate LIV, 344, lateral aspect of male hypopygium.) . . . . *T. iroquois* Alex.

Wings not colored as above 36

36. Wing apex infuscated; a dark spot at the origin of the sector; male hypopygium with the ninth tergite (Plate LII, 317) prominent, deeply notched, the lateral lobes acute; medium-sized, wing 18 mm. or less; antennae bicolorous. [Berl. Ent. Ztschr., vol. 7, p. 288. 1863.] (Plate XLVII, 239, wing.) . . . . *T. submaculata* Loew

Not as above; if the wing pattern is as described (*valida* group), the size is much larger — wing of male 20 mm. 37

37. Large, wing of male 20 mm.; wings with the apices light or dark brownish gray; male hypopygium greatly enlarged (*valida* group) 38

Smaller, wing of male under 18 mm.; wings with a heavy brown and white or grayish brown and white pattern 39

38. Ninth tergite (Plate LI, 303) with the lateral lobes more slender and pronounced; eighth sternite without a long brush of hairs; wing apex darker, brownish. [Berl. Ent. Ztschr., vol. 7, p. 287. 1863.] (Plate XLVII, 237, wing; the reproduction of the figure is much too dark.) . . . . *T. valida* Loew

Ninth tergite (Plate LI, 304) with the lateral lobes shorter and less evident; eighth sternite with a tuft of long yellow hairs; wing apex light gray, scarcely darker than the basal part of the wing. [Journ. N. Y. Ent. Soc., vol. 9, p. 113. 1901.] (Plate LIV, 345, lateral aspect of male hypopygium.) . . . . *T. hirsuta* Doane

39. Ninth tergite of the male with a dorsal black chitinized projection lying transversely at about midlength of the sclerite (in *T. longiventris* and others); remainder of the sclerite not chitinized 40

Ninth tergite of the male not chitinized, or else variously chitinized, either on the caudal margin, on the lateral margins, or with a conical tooth on the dorsal surface — in which case (*T. balioptera*) the cephalic and lateral margins are heavily chitinized and toothed 41

40. Antennae bicolorous, the basal swelling of the flagellar segments black, the pedicels yellow; prescutum fawn-colored, with four light gray stripes partly margined with dark brown; prescutal interspaces with abundant brown dots; lateral margins of the abdominal segments broadly pale grayish silvery; male hypopygium with the ninth tergite (Plate L, 285) having the lateral lobes rounded, the median caudal notch indistinct. [Berl. Ent. Ztschr., vol. 7, p. 278. 1863.] (Plate XLVI, 229, wing.)
T. longiventris Loew

Antennae unicolorous, the flagellar segments nearly uniform thruout; prescutum dull gray, with four dark brown stripes; lateral margins of the abdominal segments narrowly silvery; male hypopygium with the ninth tergite (Plate L, 286) having a deep U-shaped notch on the caudal margin. [Can. Ent., vol. 48, p. 46–48. 1916.]
T. caroliniana Alex.

41. Ninth tergite small, the caudal margin evenly rounded by a broad concavity which is very heavily chitinized; flagellar segments of antennae very deeply incised beneath, producing a serrated appearance 42

Ninth tergite not as above 43

42. Coloration bluish gray, including the abdomen; ninth tergite (Plate L, 284) with the caudal margin bluntly toothed. [Ross's Voyage to the Arctic Regions, p. 77, pl. A, fig. 15. 1831.] . . . . *T. arctica* Curt.

Coloration brown, the abdomen dull brownish yellow with an interrupted dorsal stripe; ninth tergite (Plate L, 283) short and broad, the caudal margin heavily chitinized, deeply concave, and slightly roughened in places, the lateral angles produced into conspicuous chitinized points. [Berl. Ent. Ztschr., vol. 7, p. 278. 1863.] (Plate LIV, 338, lateral aspect of male hypopygium.) . . . . *T. septentrionalis* Loew

43. Ninth tergite (Plate L, 280) small, heavily chitinized, shiny black, the caudal margin with a deep U-shaped notch, a second tooth on either side, subbasal in position; wing of male 17.5 mm.; head light gray, with a narrow, impressed median line; antennae with the first three flagellar segments indistinctly bicolorous, the remainder uniformly dark brown; abdomen orange, with an interrupted dorso-median stripe. [Berl. Ent. Ztschr., vol. 8, p. 60. 1864.] (Plate LIV, 339, lateral aspect of male hypopygium.) *T. centralis* Loew

Ninth tergite larger, not as above 44

44. Ninth tergite (Plate L, 279) heavily chitinized, black, hollowed out in a shallow saucer, the dorsal surface near the caudal margin with a prominent median tooth that is directed backward; margin of the saucer denticulate, more strongly behind; wing 16.8 mm.; head light gray; thorax dull gray, the prescutal stripes margined with brown. [Berl. Ent. Ztschr., vol. 7, p. 284. 1863.] (Plate XLVI, 227, wing; Plate LIV, 337, lateral aspect of male hypopygium.) . . . . *T. balioptera* Loew

Ninth tergite not as above 45

45. Ninth tergite (Plate L, 282) very large and extensive, narrowed slightly toward the apex, which consists of a flattened yellowish margin bearing a deep tho small median notch, the broad adjacent lobes with about three tiny teeth, the outermost one the largest; the part of the tergite behind the yellow caudal margin elevated, black, and including the basal two-thirds of the segment; wing 15 mm.; antennae blackish; prescutum light grayish brown, with about five dark brown stripes; abdominal segments dark brownish black, the caudal margin of each segment bright yellow, the lateral margins broadly gray; wings with a heavy pattern; a conspicuous dark spot at the base of the wing. [Berl. Ent. Ztschr., vol. 8, p. 57. 1864.] . . . . *T. ternaria* Loew

Ninth tergite not as above 46

46. Ninth tergite (Plate L, 281) telescoped beneath segments 7 and 8; the sclerite not chitinized, very broad and short, the caudal margin broadly concave and provided with a uniform fringe of long yellow hairs; wing 15.7 mm.; antennae somewhat bicolorous, the basal enlargement of the flagellar segments dark brown, the remainder of each segment a little paler; prescutum whitish gray, with broad dull gray stripes narrowly and indistinctly margined with brown; abdomen dull yellow, with an indistinct dorso-median stripe which broadens out on segments 6 to 8; less distinct submarginal stripes on the sides of the abdomen. [Berl. Ent. Ztschr., vol. 8, p. 59. 1864.] (Plate LIV, 341, lateral aspect of male hypopygium.) . . . . *T. canadensis* Loew

Ninth tergite not as above 47

47. Ninth tergite (Plate L, 276) large, pale, not chitinized, with two rounded lobes separated by a narrow, deep notch; antennae elongate, the segments of the flagellum not incised beneath; ventro-caudal angle of each pleurite bearing a prominent, pale, fleshy lobe. [Berl. Ent. Ztschr., vol. 7, p. 286. 1863.] (Plate XLV, 212, wing.) *T. angustipennis* Loew

Ninth tergite not as above, more or less chitinized caudally; antennae shorter, the flagellar segments deeply incised beneath 48

48. Ninth tergite (Plate L, 277) with a broad median chitinized tooth on the caudal margin; adjacent lateral lobes terminating in small, acute, chitinized points; antennae moderate in length, extending slightly beyond the wing root; prescutum fawn-colored, with four broad grayish brown stripes narrowly margined with brown; abdomen dull yellow with a rather indistinct brownish median stripe which is clearer behind. [Berl. Ent. Ztschr., vol. 7, p. 283. 1863.] . . . . *T. serta* Loew

Ninth tergite (Plate L, 278) with a very broad, pale, median lobe; adjacent lateral lobes very prominent, directed caudad and slightly inward, the tips truncated and chitinized; coloration pale, yellowish, the lateral prescutal stripes and the scutal lobes grayish; the median prescutal stripe paler, more brownish; abdomen without distinct darker stripes; wing pattern pale. [*T. senega* Alex., Insec. Inscit. Menst., vol. 3, p. 128, 1915. *T. pallida* Loew, preoccupied, Berl. Ent. Ztschr., vol. 7, p. 284, 1863.] (Plate XLV, 213, wing.) . . . . *T. senega* Alex.

49. Wing pattern dark brown sparsely marked with white, the dark brown including the wing apex and the anal and cubital cells, the white as a broad band before the cord and a blotch beyond the stigma; antennae bicolorous; prescutum with four stripes, the middle pair bifid at the anterior end; abdomen with three broad brown stripes; femora broadly tipped with dark brown (*fuliginosa* group). [*Ctenophora fuliginosa* Say. Journ. Acad. Nat. Sci. Phila., vol. 3, p. 18. 1823.] (Plate XLVIII, 246, wing of female.) . . . . *T. fuliginosa* (Say)

Wing pattern paler, brown or gray with the white more extensive 50

50. Only the tergal valves of the female ovipositor present, these lying transversely conspicuously serrated along their outer edge (*arctica* group) 51

All four valves of the ovipositor present, not serrated along their outer edge 54

51. Abdomen gray or brownish gray 52

Abdomen orange or orange-yellow on the basal tergites 53

52. Coloration blue-gray; wing pattern pale, the brown and gray markings diffuse and ill-defined; length 24 mm. [Ross's Voyage to the Arctic Regions, p. 77, pl. A, fig. 15. 1831.] . . . . *T. arctica* Curt.

Coloration light gray, the abdomen grayish brown with three indistinct brown stripes; wing pattern heavy, tessellated white and brown; antennae dark brown; head dark gray with a narrow brown median line; prescutum with three broad gray stripes margined with brown; length 27 mm. [*T. labradorica* Alex., Insec. Inscit. Menst., vol. 3, p. 128, 1915. *T. tesselata* Loew, preoccupied, Berl. Ent. Ztschr., vol. 7, p. 277, 1863.] (Plate XLVI, 228, wing.) . . . . *T. labradorica* Alex.

53. Abdomen very elongated; length of female over 30 mm.; antennae bicolorous; thoracic interspaces with tiny blackish dots. [Berl. Ent. Ztschr., vol. 7, p. 278. 1863.] (Plate XLVI, 229, wing.) . . . . *T. longiventris* Loew

Abdomen short, normal; length of female 25 mm.; wing pattern pale. [Berl. Ent. Ztschr., vol. 8, p. 58. 1864.] . . . . *T. serrulata* Loew

54. Large species, wing over 22 mm. (*valida* group). [Berl. Ent. Ztschr., vol. 7, p. 287. 1863.] . . . . *T. valida* Loew

[Journ. N. Y. Ent. Soc., vol. 9, p. 113. 1901.] . . . . *T. hirsuta* Doane

Smaller, wing under 20 mm. 55

55. Wings gray, the apex darker; a broad white obliterative streak before the cord extending into the base of cell M_4; a brown spot at the origin of *Rs*; antennae bicolorous; shiny basal plate of the dorsal tergal valves of the ovipositor very elongate, as long as the valves themselves and longer than the seventh and eighth tergites taken together. [Berl. Ent. Ztschr., vol. 7, p. 288. 1863.] (Plate XLVII, 239, wing.) . . . *T. submaculata* Loew

Wings not so colored 56

56. Wings light gray, with a dark brown oval stigma and a broad grayish brown crossband extending from *Rs* across the wing; antennae bicolorous, at least basally; thoracic pleura with two longitudinal brown stripes. [*T. hermannia* Alex., Proc. Acad. Nat. Sci. Phila., p. 480, 1915. *T. fasciata* Loew, preoccupied, Berl. Ent. Ztschr., vol. 7, p. 279, 1863.] (Plate XLV, 211, wing.) . . . . *T. hermannia* Alex.

Wings not so colored 57

57. Wings grayish subhyaline, the apex narrowly and irregularly dark brown, the cord seamed with dark grayish brown; antennae dark brown thruout; thorax light gray, with four dark gray stripes which are margined with dark brown; thoracic pleura clear light gray, dorso-pleural membrane yellowish. [*T. iroquois* Alex., Insec. Inscit. Menst., vol. 3, p. 128, 1915. *T. cincta* Loew, preoccupied, Berl. Ent. Ztschr., vol. 7, p. 288, 1863.] (Plate XLVIII, 252, wing.) . . . . *T. iroquois* Alex.

Wings not so colored 58

58. Wings with about four large dark brown blotches along the radial vein, the second at the origin of the sector, the third at the stigma; wing apex narrowly light brown; wing about 16.5 mm.; antennae bicolorous; head dark gray, with a narrow, impressed, median line; prescutum dull gray with four clearly defined bright brown stripes; abdomen dull yellow with three dark brown stripes; tergal valves of ovipositor acicular. [Berl. Ent. Ztschr., vol. 8, p. 58. 1864.] (Plate XLVII, 233, wing.) *T. macrolabis* Loew

Wings not so colored...59

59. Thorax with the prescutal stripes concolorous with the ground color of the thorax, the lateral stripes broadly margined in front and on the sides with dark brown; median stripe broadly margined on the sides; wings with a variegated brown, gray, and white pattern (*hebes* group)...60

Thorax not so colored...62

60. Antennae bicolorous, at least basally. [Berl. Ent. Ztschr., vol. 7, p. 285. 1863.] (Plate XLVIII, 249, wing.).......................................*T. hebes* Loew

Antennae unicolorous...61

61. Cell R_5 of wings usually white or largely so; antennae shorter. [Berl. Ent. Ztschr., vol. 7, p. 281. 1863.].......................................*T. grata* Loew

Cell R_5 of wings infuscated except basally; antennae longer. [Berl. Ent. Ztschr, vol. 8, p. 60. 1864.].......................................*T. latipennis* Loew

62. Wings with a pale gray and hyaline pattern; cell *Sc* uniformly dark brown; *m-cu* cross-vein close to the fork of *M* (*marmorata* group).......................................63

Wings with the pattern darker gray and brown; if the pattern is pale, the cell *Sc* is not dark brown and the *m-cu* cross-vein is not close to the fork of *M* (*angustipennis* group)...64

63. Stripes on the prescutum ending at the level of the pseudosutural foveae, the median pair blunt at their anterior ends. [Berl. Ent. Ztschr., vol. 7, p. 279. 1863.] (Plate XLVIII, 250, wing.).......................................*T. fragilis* Loew

Median stripes of the prescutum extending about to the anterior margin of the sclerite, deeply bifid at their anterior ends. [Berl. Ent. Ztschr., vol. 7, p. 280. 1863.] *T. ignobilis* Loew

64. Abdominal tergites dark slate gray, narrowly margined caudally with bright orange-yellow; length 24 mm.; wing 18 mm.; antennae dark brownish black thruout; head dark gray with a narrow brown median stripe; prescutum brownish gray, the stripes darker brown, not clear-cut; thoracic pleura clear gray; wing pattern heavy; a distinct dark brown spot at the base of the wing. [Berl. Ent. Ztschr., vol. 8, p. 57. 1864.] *T. ternaria* Loew

Coloration not as above...65

65. Valves of ovipositor short, about as long as the fifth tergite. [*T. senega* Alex., Insec. Inscit. Menst., vol. 3, p. 128, 1915. *T. pallida* Loew, preoccupied, Berl. Ent. Ztschr., vol. 7, p. 284, 1863.] (Plate XLV, 213, wing.) ....*T. senega* Alex.

Valves of ovipositor elongate, acicular, much longer than the fifth tergite alone.......66

66. Abdomen orange, with three dark brownish black stripes; no basal gray ring on the abdominal tergites. [Berl. Ent. Ztschr., vol. 7, p. 286. 1863.] (Plate XLV, 212, wing.).......................................*T. angustipennis* Loew

Abdomen not so colored; a narrow basal ring on the abdominal tergites, grayish and destitute of the scattered hairs found on the remainder of the segment..........67

67. Abdomen long and slender, indistinctly trivittate with brown, the stripes interrupted by the smooth basal areas of the segments. [Berl. Ent. Ztschr., vol. 7, p. 283. 1863.] *T. serta* Loew

Abdomen with the lateral stripes broad, continuous; lateral margins of the segments broadly pale grayish. [*T. ignota* Alex., Insec. Inscit. Menst., vol. 3, p. 128, 1915. *T. discolor* Loew, preoccupied, Berl. Ent. Ztschr., vol. 7, p. 282, 1863.] *T. ignota* Alex.

68. Cell *1st* M_2 open by the atrophy of the medial cross-vein; wing of female 10.5 mm.; coloration grayish brown, the thoracic stripes indistinct. [*Tipula aperta* Alex., Can. Ent., vol. 50, p. 62, 1918. *T. imperfecta* Alex., preoccupied, Proc. Acad. Nat. Sci. Phila., p. 484–485, pl. 16, fig. 9, 1915.] (Plate XLVII, 235, wing.) . . . *T. aperta* Alex.
Cell *1st* M_2 closed 69
69. Color of wings almost uniformly dark brown (females only) 70
Color of wings hyaline, pale grayish, or yellowish 71
70. Size small, wing of female about 8 mm.; abdominal tergites uniformly dark brown thruout; cell *1st* M_2 pointed at its outer end, due to the extreme shortening of the medial cross-vein. [Journ. Acad. Nat. Sci. Phila., vol. 6, p. 151. 1829.] . . . . . . *T. annulicornis* Say
Size larger, wing of female over 10 mm.; abdominal tergites dark brown, with broad, bright yellow, median triangles, the points directed forward; cell *1st* M_2 not pointed at its distal end, the medial cross-vein of normal length, nearly as long as the petiole of cell M_1. [Proc. Acad. Nat. Sci. Phila., p. 476–479, pl. 16, figs. 7, 8. 1915.] (Plate XLVIII, 244, wing.) . . . . . *T. taughannock* Alex.
71. Color of thorax light gray or blue-gray, with distinct clear-cut brown or black stripes; body clothed with long, pale hair; wing over 14 mm. Northern species 72
Color of thorax brown, yellow, or gray; if grayish (*T. dejecta*), the wing is under 12 mm. and the body is not clothed with long, pale hair 73
72. Color of thorax dull light gray, with four light brown stripes; median vitta of the head indistinct; dorsal abdominal vitta narrow; eighth abdominal tergite of female with the margins flattened and conspicuously expanded; tergal valves of the ovipositor long, pale. [Proc. Acad. Nat. Sci. Phila., p. 482–484, pl. 21, fig. 85. 1915.] *T. piliceps* Alex.
Color of thorax blue-gray, with the stripes almost black, broad, the median pair tending to become confluent; median vitta of the head distinct; dorsal abdominal vitta broader, more diffuse; eighth abdominal tergite of female with the margins not conspicuously expanded; tergal valves of the ovipositor smaller; wing pale gray, stigma dark brown; antennae black thruout; ninth tergite of male deeply notched medially, the adjacent lateral lobes broad, truncated, pale; outer pleural appendages broad, pale; wing of male 14 mm. [Proc. Boston Soc. Nat. Hist., vol. 19, p. 42. 1876.] *T. besselsi* O. S.
73. Males (as known) 74
Females (as known) 103
74. Caudal margin of ninth tergite (Plate L, 288) with a compressed median lobe projecting caudad of the short lateral lobes; distal end of cell *1st* M_2 pointed, cross-vein *m* very short; size very small, wing of male under 8 mm.; antennae elongated, bicolorous; thoracic stripes indistinct. [Journ. Acad. Nat. Sci. Phila., vol. 6, p. 151. 1829.] (Plate XLVIII, 243, wing; Plate LIII, 335, lateral aspect of male hypopygium.) *T. annulicornis* Say
Caudal margin of ninth tergite without a compressed median lobe projecting beyond the lateral lobes; distal end of cell *1st* M_2 not pointed; size larger, wing of male over 10 mm 75
75. Sclerites of ninth segment fused into a nearly complete ring; caudal margin of the tergite truncate with a broad, depressed, median lobe or with two approximated slender, parallel lobes, one on either side of the median line 76
Sclerites of ninth segment not fused, at least the tergite distinct; ninth tergite without median lobes on the caudal margin 80
76. Ninth tergite with two slender, finger-like lobes on the caudal margin (*tephrocephala* group) 77
Ninth tergite with a single broad median lobe or with two short blunt lobes on the caudal margin (*perlongipes* group) 78
77. Antennal flagellar segments bicolorous, the basal swelling of each segment yellow, the pedicel dark. [Berl. Ent. Ztschr., vol. 8, p. 62. 1864.] (Plate XLVI, 221, wing; Plate XLIX, 271, ninth tergite.) . . . . . *T. tephrocephala* Loew

Antennal flagellar segments bicolorous, the basal swelling of each segment black, the pedicel yellow. [Proc. Acad. Nat. Sci. Phila., p. 485–487, pl. 16, fig. 10. 1915.] (Plate XLVI, 222, wing; Plate XLIX, 272, ninth tergite; Plate LIII, 325, eighth sternite.) . . . . *T. cayuga* Alex.

78. Size small, wing 12 mm.; thoracic dorsum dull gray, with four brownish stripes; antennae unicolorous, dark brown; pleura clear light gray; sides of postnotum light yellow; ninth tergite (Plate XLIX, 270) with two broad lobes, the notch between deep. [Journ. N. Y. Ent. Soc., vol. 9, fig. 99. 1901.] (Plate XLVI, 225, wing.) *T. sulphurea* Doane

Size larger, wing 14 mm. or over; thoracic dorsum not colored as above 79

79. Antennae bicolorous; thoracic dorsum dull yellow with three brown stripes, the lateral pair less distinct than the median one; legs long; male hypopygium with the median lobe of the ninth tergite (Plate XLIX, 268) entire or the bifid nature barely indicated. [*T. perlongipes* Johns., Proc. Boston Soc. Nat. Hist., vol. 34, p. 131, 1909. *T. filipes* Walk., preoccupied, List Dipt. Brit. Mus., p. 65, 1848.] (Plate XLVI, 223, wing.) . . . . *T. perlongipes* Johns.

Antennae unicolorous or nearly so; thorax gray, with three broad, more or less distinct, stripes, the median one with a delicate dark brown line; legs short; male hypopygium with the median lobe of the ninth tergite (Plate XLIX, 269) bifid. [Proc. Acad. Nat. Sci. Phila., p. 480–482, pl. 16, fig. 6. 1915.] (Plate XLVI, 224, wing; Plate LIII, 331, lateral aspect of male hypopygium.) . . . . *T. kennicotti* Alex.

80. Ninth tergite (Plate LII, 309) large, the caudal margin with a small rounded notch on either side of a small acute median tooth; eighth sternite with broad, fleshy, lateral lobes directed proximad and with the ventral inner angle produced into a chitinized point and clothed with long yellow hairs; median area of the sternite with a prominent chitinized tooth on either side of the median line, broadly separated by a distance greater than the diameter of one tooth; size large, wing 18–20 mm.; antennae bicolorous. [Berl. Ent. Ztschr., vol. 7, p. 292. 1863.] (Plate XLVII, 236, wing.) *T. umbrosa* Loew

Ninth tergite not as described; eighth sternite, if with fleshy lateral lobes (*T. australis*, *T. valida*, and others), without two chitinized teeth on the caudal margin of the sternite 81

81. Size large, wing over 20 mm.; male hypopygium greatly enlarged; eighth sternite with elongate lateral lobes and a flattened median lobe (*valida* group; included also in the section with marked wings, because the tips of the wings are usually of a darker gray than the basal part) 82

Size smaller, wing under 18 mm.; male hypopygium not greatly enlarged; eighth sternite not as above 83

82. Ninth tergite (Plate LI, 303) with the lateral lobes more slender and pronounced; eighth sternite without a long brush of hairs. [Berl. Ent. Ztschr., vol. 7, p. 287. 1863.] (Plate XLVII, 237, wing.) . . . . *T. valida* Loew

Ninth tergite (Plate LI, 304) with the lateral lobes shorter and blunter; eighth sternite with a brush of long yellow hairs. [Journ. N. Y. Ent. Soc., vol. 9, p. 113. 1901.] *T. hirsuta* Doane

83. Wing apex a little grayer than the basal cells of the wings; a brown spot at the origin of the sector; male hypopygium with the ninth tergite (Plate LII, 317) large, deeply split by a broad V-shaped notch, the lateral lobes acutely pointed. (This species is included also in the section with marked wings, because the tips of the wings are usually of a darker gray than the basal part.) [Berl. Ent. Ztschr., vol. 7, p. 288. 1863.] (Plate XLVII, 239, wing.) . . . . *T. submaculata* Loew

Wing apex unicolorous or nearly so; ninth tergite not as described 84

84. Antennae unusually elongated, if bent backward extending to the base of the fifth abdominal segment; ninth tergite (Plate LI, 290) with the lateral lobes subacute, the median lobe situated in a deep, shield-shaped depression; eighth sternite unarmed; antennae unicolorous; abdominal tergites bright yellow, with three distinct brownish

black stripes which are confluent across the bases and less distinctly across the apices of tergites 2 to 5; wing 15 mm.; cell *1st* M_2 elongate; wings yellowish subhyaline, the obliterative streak very reduced, appearing as a spot before the stigma and a linear dash in the base of cell *1st* M_2 and the end of cell *R*. [Proc. Acad. Nat. Sci. Phila., p. 476–479, pl. 16, figs. 7, 8. 1915.] (Plate LIII, 336, lateral aspect of male hypopygium.) . . . . *T. taughannock* Alex.

Antennae shorter, not extending beyond the base of the abdomen; ninth tergite not as described; if at all similar (*T. monticola*), the eighth sternite armed with brushes of hairs or bristles 85

85. Ninth tergite (Plate LI, 301) small, with the caudal margin bearing a blunt median lobe and with a prominent divergent horn on either side; thoracic pleura clear light gray; eighth sternite unarmed; size small, wing 11.5 mm.; antennae uniform dark brown. [Ins. Saunders., vol. 1, Dipt., p. 442. 1856.] (Plate XLVIII, 251, wing.) *T. dejecta* Walk.

Ninth tergite not as above 86

86. Ninth tergite (Plate LII, 308) small, the caudal margin with a broad V-shaped notch; ninth pleurite produced caudad into a short, flattened, subspatulate lobe; eighth sternite extensive, narrowed behind, the caudal margin broadly U-shaped and bearing a row of prominent yellow hairs; color light gray, the thorax marked with brown; wing about 16 mm. [Proc. Acad. Nat. Sci. Phila., p. 488–490, pl. 16, fig. 12. 1915.] (Plate XLVII, 234, wing.) . . . . *T. loewiana* Alex.

Hypopygial characters not as above 87

87. Coloration of thoracic pleura light gray; thoracic dorsum gray or grayish, with brown stripes 88

Coloration of thoracic pleura yellow, in some cases whitish pollinose; dorsum yellow or brown 90

88. Ninth sternite with a stout pendulous lobe directed ventrad, bearing a dense tuft or pencil of long reddish hairs; eighth sternite large, prominent, extending far caudad and its concavity forming a sheath for the base of the ninth sternite, the lateral angles bearing dense tufts of long, reddish-silvery hairs which are decussate; between these lobes a broad median projection, the lateral angles of which are slightly recurved and the caudal margin is broadly concave; color grayish, with distinct dark brown thoracic stripes; wings light brown, the tips a little darker; a large vitreous spot before and beyond the stigma; wing of male 12.6 mm. Arctic species. [Proc. Acad. Nat. Sci. Phila., p. 496–497. 1915.] (Plate LII, 314, ninth tergite.) . . . *T. penicillata* Alex.

Hypopygial characters not as above. Austral species 89

89. Antennae short, the flagellar segments deeply constricted beyond the basal enlargement; six brown stripes on the mesonotal prescutum; male hypopygium with the ninth tergite (Plate LII, 305) almost straight across the caudal margin, with a deep and narrow impressed median furrow; lobes of the caudo-lateral angles of the ninth sternite pendulous, directed ventrad, the apices clothed with short golden hairs; eighth sternite (Plate LIII, 326) with four conspicuous lobes, the outer pair very broad and flattened, their apices oblique, the inner pair being the divaricate ends of a median process on the caudal margin of the sternite, their apices clothed with a dense brush of golden-yellow hair. [Journ. N. Y. Ent. Soc., vol. 9, p. 104–105. 1901.] . . . *T. australis* Doane

Antennae longer, the flagellar segments not constricted beyond the basal enlargement; three brown stripes on the mesonotal prescutum; male hypopygium with the ninth tergite (Plate LII, 306) having the caudal margin deeply and broadly notched medially; lobes of the caudo-lateral angles of the ninth sternite not pendulous, directed inward; eighth sternite (Plate LIII, 327) without lobes on the caudal margin. [Proc. Acad. Nat. Sci. Phila., p. 501–504, pl. 17, fig. 19. 1915.] (Plate XLVII, 238, wing.) *T. dietziana* Alex.

90. Coloration bright brownish yellow, the thorax with dark brown stripes; pleura dull yellow, whitish pollinose; male hypopygium with the ninth tergite (Plate LII, 307) broadly concave caudally, the lateral angles not prominent; antennae with the three

basal segments light yellow, the remainder of the organ more or less distinctly bicolorous; abdomen dull yellow, the tergites with a conspicuous dark brown stripe; wing 12 mm. [Proc. Acad. Nat. Sci. Phila., p. 475–476, pl. 16, fig. 5. 1915.] (Plate XLVIII, 253, wing; Plate LIV, 346, lateral aspect of male hypopygium.) . . . . *T. mainensis* Alex.
Coloration not as above, the thoracic stripes not dark brown; hypopygium not as above 91

91. Nasus short; cell *1st* M_2 of wings very small and pentagonal; male hypopygium with the ninth tergite usually tumid, unarmed or provided with horns; in species in which the tergite is not conspicuously swollen and tumid (*T. parshleyi*), the cell *1st* M_2 is small and pentagonal, as above; in species in which the cell 1*st* M_2 is longer (*T. johnsoniana*), the ninth tergite is tumid tho unarmed (*bicornis* group) 92
Nasus usually longer; cell *1st* M_2 of wings not small and pentagonal; male hypopygium with the ninth tergite not tumid (*translucida* group) 96

92. Ninth tergite (Plate LII, 321) not tumid; eighth sternite very long, sheathing the ninth sternite beneath, the tip with two chitinized points on either side. [Proc. Acad. Nat. Sci. Phila., p. 510–512, pl. 17, fig. 23. 1915.] (Plate LV, 354, lateral aspect of male hypopygium.) . . . . *T. parshleyi* Alex.
Ninth tergite tumid; eighth sternite shorter, not closely applied to ninth sternite for the entire length of the latter, the apex without chitinized points 93

93. Ninth tergite (Plate LII, 320) with four lobes or horns. [Journ. N. Y. Ent. Soc., vol. 9, p. 112–113. 1901.] (Plate XLVI, 231, wing; Plate LV, 353, lateral aspect of male hypopygium.) . . . . *T. megaura* Doane
Ninth tergite with two horns or without horns 94

94. No horns on the tergite (Plate LII, 318). [Proc. Acad. Nat. Sci. Phila., p. 505–506, pl. 17, fig. 20. 1915.] (Plate LV, 351, lateral aspect of male hypopygium.) *T. johnsoniana* Alex.
Horns on the tergite 95

95. Horns on tergite (Plate LII, 319) directed upward. [16th Rept. State Ent. Ill., p. 78, pl. 6, fig. 4. 1891.] (Plate XLVI, 230, wing; Plate LV, 350, lateral aspect of male hypopygium.) . . . . *T. bicornis* Forbes
Horns on tergite directed caudad or slightly ventrad. [Proc. Acad. Nat. Sci. Phila., p. 507–508, pl. 17, fig. 21. 1915.] (Plate LV, 352, lateral aspect of male hypopygium.) *T. morrisoni* Alex.

96. Caudal margin of ninth tergite (Plate LII, 315) with three prominent lobes, the median lobe acute; antennae bicolorous; body coloration light yellow, the thoracic stripes reddish brown; abdomen with a series of about four conspicuous, rounded, brown spots along the sides; wing 13.5 mm. Southern species. [Proc. Acad. Nat. Sci. Phila., p. 487–488, pl. 16, fig. 11. 1915.] (Plate XLVII, 240, wing.) . . . . *T. triton* Alex.
Caudal margin of ninth tergite not trifid 97

97. Caudal margin of ninth tergite (Plate LII, 316) deeply notched, the lateral lobes produced into long, slightly curved horns; outer pleural lobe a conspicuous curved hook; antennae bicolorous; body coloration yellowish, the thoracic stripes very indistinct; wings yellowish; wing 17.2 mm. [Proc. Acad. Nat. Sci. Phila., p. 493–495, pl. 16, fig. 15. 1915.] (Plate XLVII, 241, wing; Plate LIII, 328, eighth sternite; Plate LV, 349, lateral aspect of male hypopygium.) . . . . *T. tuscarora* Alex.
Male hypopygium not as above 98

98. Lateral lobes of ninth tergite (Plate LII, 310) broad, squarely truncated; antennae more or less distinctly bicolorous; coloration brownish yellow; wing 18 mm. [Proc. Acad. Nat. Sci. Phila., p. 490–492, pl. 16, fig. 13. 1915.] (Plate XLVII, 242, wing.) *T. mingwe* Alex.
Lateral lobes of ninth tergite not squarely truncated, more or less pointed or rounded 99

99. Lateral lobes of ninth tergite pointed 100
Lateral lobes of ninth tergite rounded 102

100. Inner pleural appendage produced caudad into an elongate, subacute, pale, fleshy lobe 101
Inner pleural appendage complex, consisting of a slender caudal lobe which is directed backward and pointed, and a cephalic lobe which is compressed, black, and heavily chitinized along the margin; coloration yellowish; antennae bicolorous; head light gray; thoracic stripes rather indistinct, brownish orange; ninth tergite (Plate LII, 312) with the lateral angles tipped with a cylindrical, conical point; median lobe prominent, convex, rounded; eighth sternite large, prominent, projecting caudad, the posterior margin with a rounded notch bearing a dense tuft of long, silvery hairs on each side of the mid-line; wing of male 18–19 mm. [Proc. Acad. Nat. Sci. Phila., p. 492–493, pl. 16, fig. 14. 1915.] (Plate LV, 347, lateral aspect of male hypopygium.) . . . . *T. monticola* Alex.
101. Antennal flagellum dark brown; body coloration light gray; ninth tergite with the lateral angles subangular, not approximated; median lobe not prominent, shiny; thorax with three broad brown stripes; wing 12.5 mm. Southern species. [Insec. Inscit. Menst., vol. 3, p. 134–136. 1915.] . . . . *T. catawba* Alex.
Antennal flagellum bicolorous; body coloration yellowish, the thoracic stripes indistinct; ninth tergite (Plate LII, 313) with the acute lateral lobes approximated, the space between narrow. [Journ. N. Y. Ent. Soc., vol. 9, p. 109. 1901.]
T. translucida Doane
102. Abdominal tergites 2 to 5 with a brown subbasal spot on the lateral margin; ninth tergite of male with a deep rectangular notch, the median area not convex; antennae indistinctly bicolorous; thorax brownish yellow without distinct stripes; wing 12.6 mm. Southern species. [Proc. Acad. Nat. Sci. Phila., p. 495–496, pl. 16, fig. 16. 1915.] (Plate LV, 348, lateral aspect of male hypopygium.) . . . . *T. seminole* Alex.
Abdominal tergites without a brown subbasal spot on the lateral margin; ninth tergite of male (Plate LII, 311) with the lateral angles conspicuous, the apices bluntly rounded; median area broad, highly convex to obtusely pointed, shiny chestnut brown to yellow; antennae usually bicolorous; thorax light brownish yellow, the stripes a little darker, pale brown; wing about 13 mm. [Insec. Inscit. Menst., vol. 3, p. 134–135. 1915.] . . . . *T. georgiana* Alex.
103. Lobes of ovipositor blunt, unchitinized . . . . *bicornis* group
Lobes of ovipositor pointed, chitinized . . . . Females of other species with unmarked wings
No attempt is made here to separate the females of the species with unmarked wings; many of the species have not been definitely associated with their mates and are not really known. In all cases in which pairs of flies are taken in copula, the two sexes should be pinned on the same pin, the male above. In many groups of the genus it is quite impossible to separate the females on the characters known at present.

Since the above key was completed a few additional species of Tipula have been described. These are briefly diagnosed here in order to complete the data.

Tipula aprilina Alex. (Alexander, 1918 a: 63–64.)
Dejecta group; close to *T. dejecta.* Male hypopygium with the ninth tergite large, the posterior margin with the lateral angles produced caudad into prominent blunt lobes which are blackened and furnished with small tubercles, the caudal margin truncated; between these lateral lobes two parallel, usually longer and slightly pointed, lobes which are directed slightly ventrad, one on either side of the median line; outer pleural appendage very small and inconspicuous, elongate-cylindrical, yellowish; inner pleural appendage elongate, narrow; margins of ninth sternite not widely separated beneath, carinate, and with a narrow V-shaped posterior notch bearing a pair of small, fleshy lobes. Wing of male, 11.5 mm. (Virginia, April.)

T. conspicua Dietz. (Dietz, 1917:149–150.)
Tricolor group; close to *T. eluta*. Grayish white; antennal flagellum distinctly bicolorous; thoracic stripes margined with brown, the median stripe divided by a dark line; hyaline vitta of wings reaching the outer margin; abdomen yellow, unstriped; ninth tergite with lateral pencils of hairs. Wing of male, 17 mm. (North Carolina, September.)

T. sackeniana Alex. (Alexander, 1918 a:62–63.)
Tricolor group; close to *T. tricolor*. Coloration reddish brown; antennae bicolorous; male hypopygium without a pencil of hairs on either side of median lobe of tergite. Wing of male, 15.5 mm. (New York, Maryland, Virginia, and Georgia, July and September.)

T. vicina Dietz. (Dietz, 1917:148–149.)
Tricolor group; close to *T. eluta*. Grayish brown; antennal flagellum unicolorous brown; mesonotal stripes margined with brown, the median stripe divided by a blackish line; hyaline vitta of wings extending thru cells *1st* M_2 and R_5 to margin; abdomen striped laterally. Wing of male, 13 mm. (New York, May; Michigan, July.)

T. entomophthorae Alex. (Alexander, 1918 c:385–386.)
Trivittata group; close to *T. angulata*. Mesonotal prescutum gray with three brown stripes; wings gray with a broad white crossband beyond the cord; vein R_2 persistent for its entire length; male hypopygium with the ninth tergite deeply notched medially, the lateral angles obliquely truncated. Wing of male, 15.8 mm. (North Carolina.)

T. flavibasis Alex. (Alexander, 1918 c:411–412.)
Valida group. A small, pale brownish species, easily distinguished from all its relatives by the bicolorous antennae, the basal enlargements of the segments being light yellow and the remainder black. Antennae of male long and slender, if bent backward extending to beyond base of abdomen. In coloration of antennae the species in the faunal limits of this paper is approached only by *T. tephrocephala*, a very different fly. Wing of male, 12 mm. (Kansas, July.)

T. huron Alex. (Alexander, 1918 a:66–67.)
Valida group; close to *T. submaculata*. Wings with a heavy brown pattern resembling *T. trivittata* or *T. angulata*. Wing of male, 15.6 mm. (Wisconsin, June.)

T. margarita Alex. (Alexander, 1918 b:243–244.)
General coloration of head and thorax light gray; antennae short, black, the three basal segments orange-yellow; femora with a broad subterminal yellow ring, most distinct on the fore legs; wings with four brown crossbands; abdomen yellow, the tergites with a broad dark brown median stripe and narrow sublateral stripes, the lateral margin of the tergites broadly light gray; male hypopygium with the ninth tergite large, subquadrate, with a deep median split, the ninth pleurite complete, the eighth sternite with a large tuft of yellow hairs on either side of the median line. Wing of male, 14.4 mm. (New York, June.)

T. fultonensis Alex. (Alexander, 1918 a:67.)
Arctica group; close to *T. longiventris*. Abdomen of female about one-half inch shorter than in the female of *longiventris* (16 mm.). Wing of female, 18.5 mm. (New York, June.)

T. helderbergensis Alex. (Alexander, 1918 a:64–65.)
Hebes group; close to *T. latipennis*. General color very dark; antennal flagellum uniformly brown; male hypopygium with the eighth sternite densely fringed with long golden hairs. Wing of male, 14 mm. (New York, July.)

It will be noted that many names are not included in this key to the genus Tipula, and this is because most of them are synonymous with species that are included. The principal synonymy is as follows:

T. apache Alex.	=	*T. dorsolineata* Doane
T. calva Doane	=	*T. valida* Loew
T. casta Loew	=	*T. cunctans* Say
T. cincta Loew	=	*T. iroquois* Alex.
T. costalis Say	=	*T. sayi* Alex.
T. cuspidata Doane	=	*T. submaculata* Loew
T. decora Doane	=	*T. angulata* Loew
T. discolor Loew	=	*T. ignota* Alex.
T. fasciata Loew	=	*T. hermannia* Alex.
T. filipes Walk.	=	*T. perlongipes* Johns.
T. flavicans Fabr.	=	*T. ultima* Alex.
T. fumosa Doane	=	*T. dejecta* Walk.
T. illinoiensis Alex. (female)	=	*T. senega* Alex. (male)
T. illustris Doane	=	*Stygeropis fuscipennis* Loew
T. imperfecta Alex.	=	*T. aperta* Alex.
T. inermis Doane	=	*T. umbrosa* Loew
T. infuscata Loew	=	*T. cunctans* Say
T. jejuna Johns. (female)	=	*T. annulicornis* Say
T. ottawaensis Dietz	=	*T. latipennis* Loew
T. pallida Loew	=	*T. senega* Alex.
T. speciosa Loew (male)	=	*T. fuliginosa* (Say)
T. spectabilis Doane	=	*T. macrolabis* Loew
T. suspecta Dietz	=	*T. afflicta* Dietz
T. suspecta Loew	=	*T. fragilis* Loew
T. tesselata Loew	=	*T. labradorica* Alex.
T. versicolor Loew (female)	=	*T. senega* Alex. (female)
T. winnemana Alex.	=	*T. johnsoniana* Alex.

In addition the following species, which are not recognizable from the descriptions, are omitted:

T. borealis Walk.
T. duplex Walk.
T. maculipennis Say
T. platymera Walk.
T. puncticornis Macq.
T. resurgens Walk.
T. retorta v. d. W.
T. triplex Walk.
T. vitrea v. d. W.

T. albonotata Doane is probably a good species, close to *T. trivittata* Say but with the thoracic pattern different, the prescutum with three broad brown stripes.

T. cincticornis Doane is likewise a good species, rather similar to *T. translucida* Doane (page 955) but with the outer pleural lobe longer and the pendulous appendage of the ninth sternite shorter. It differs from *T. monticola* Alex. (page 955) in the structure of the eighth sternite, the yellow head, the yellow thoracic pleura, and other characters.

T. maculipennis Say is probably *T. angustipennis* Loew but the species is in doubt. Specimens in the Harris collection of the Boston Society of Natural History are determined by Say, tho not of the original series, and these are *T. angustipennis* or close to it. However, the description of the species shows that it differs in several important respects from all specimens of *T. angustipennis* that the writer has seen, and it seems that the species must for the present remain in doubt.

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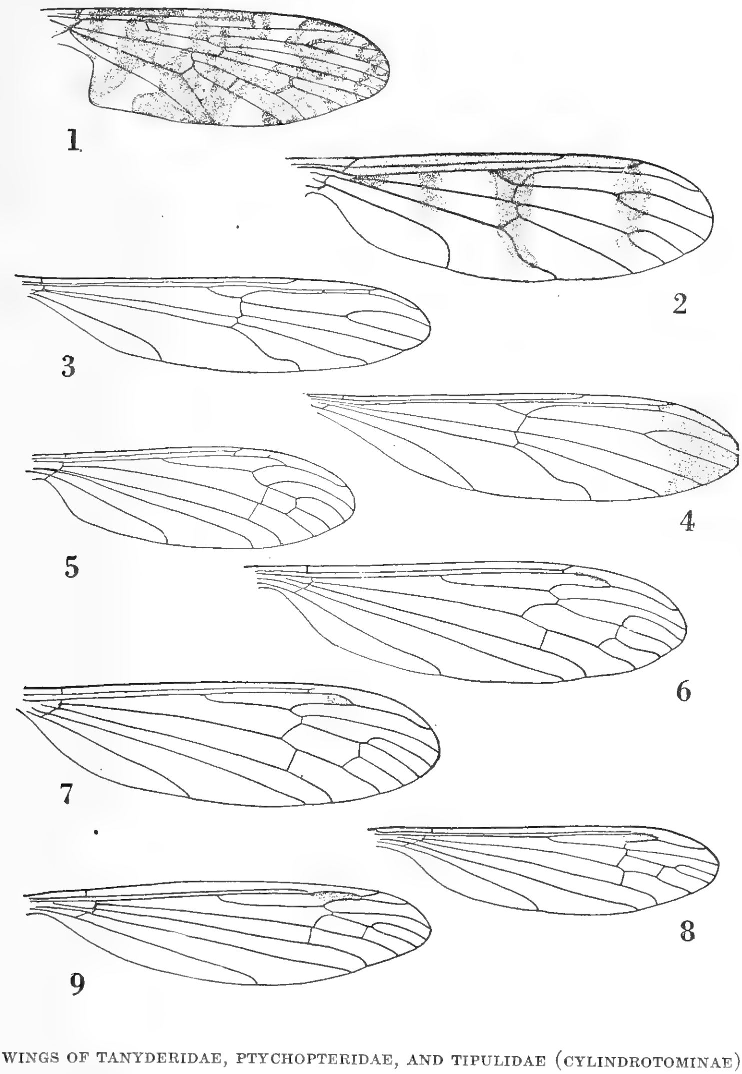
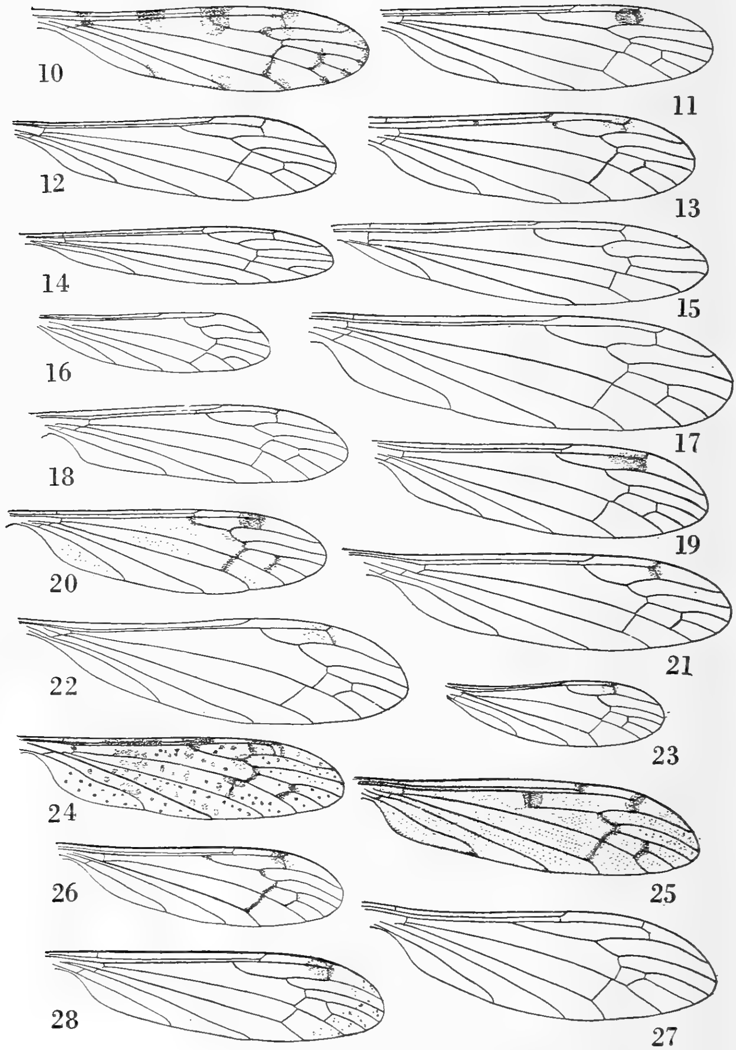


WINGS OF TANYDERIDAE, PTYCHOPTERIDAE, AND TIPULIDAE (CYLINDROTOMINAE)

1, *Protoplasa fitchii*

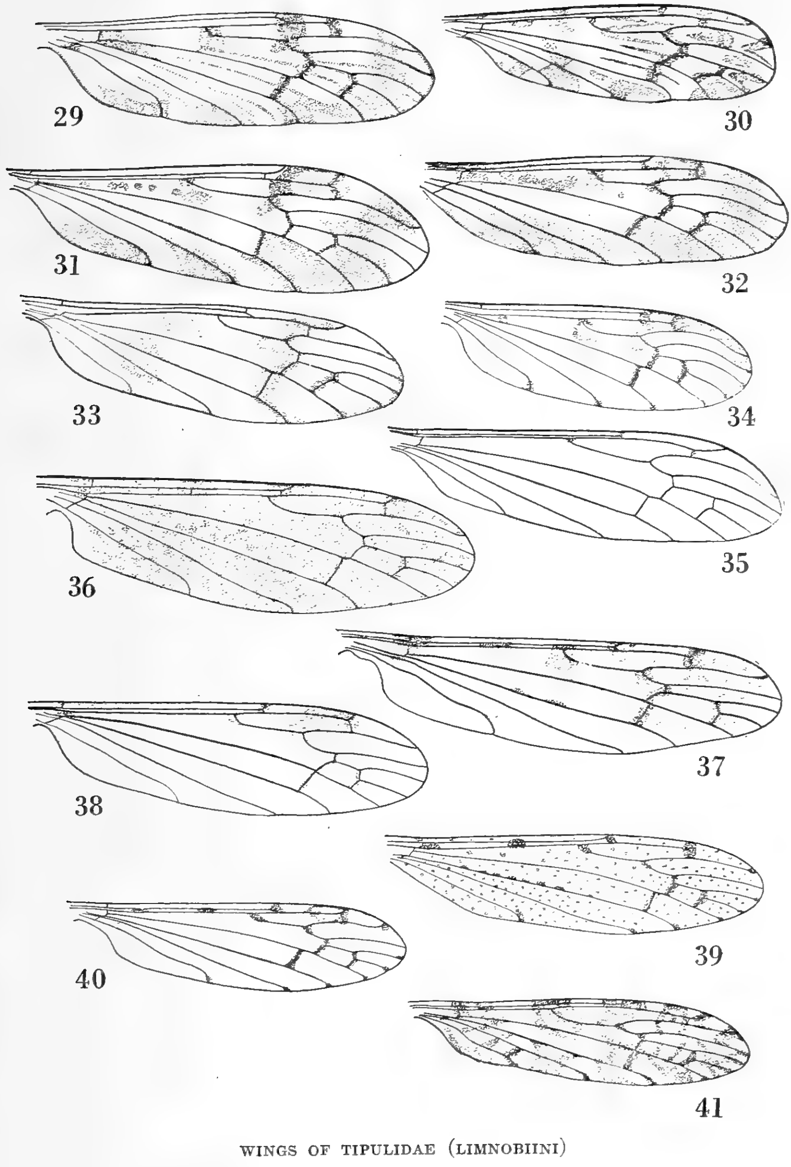
2, *Ptychoptera rufocincta*. 3, *Bittacomorpha clavipes*. 4, *Bittacomorphella jonesi*

5, *Liogma nodicornis*. 6, *Cylindrotoma americana*; 7, *C. tarsalis*. 8, *Phalacrocera tipulina*; 9, *P. neoxena*



WINGS OF TIPULIDAE (LIMNOBIINI)

10, *Geranomyia rostrata*. 11, *G. canadensis*. 12, *G. distincta*. 13, *G. diversa* 14, *Dicranomyia longipennis*. 15, *D. whartoni*. 16, *D. rostrifera*. 17, *D. haeretica*. 18, *D. halterata*. 19, *D. monticola*. 20, *D. badia*. 21, *D. liberta*. 22, *D. pudica*. 23, *D. morioides*. 24, *D. simulans*. 25, *D. rara*. 26, *D. macateei*. 27, *D. globithorax*. 28, *D. pubipennis*

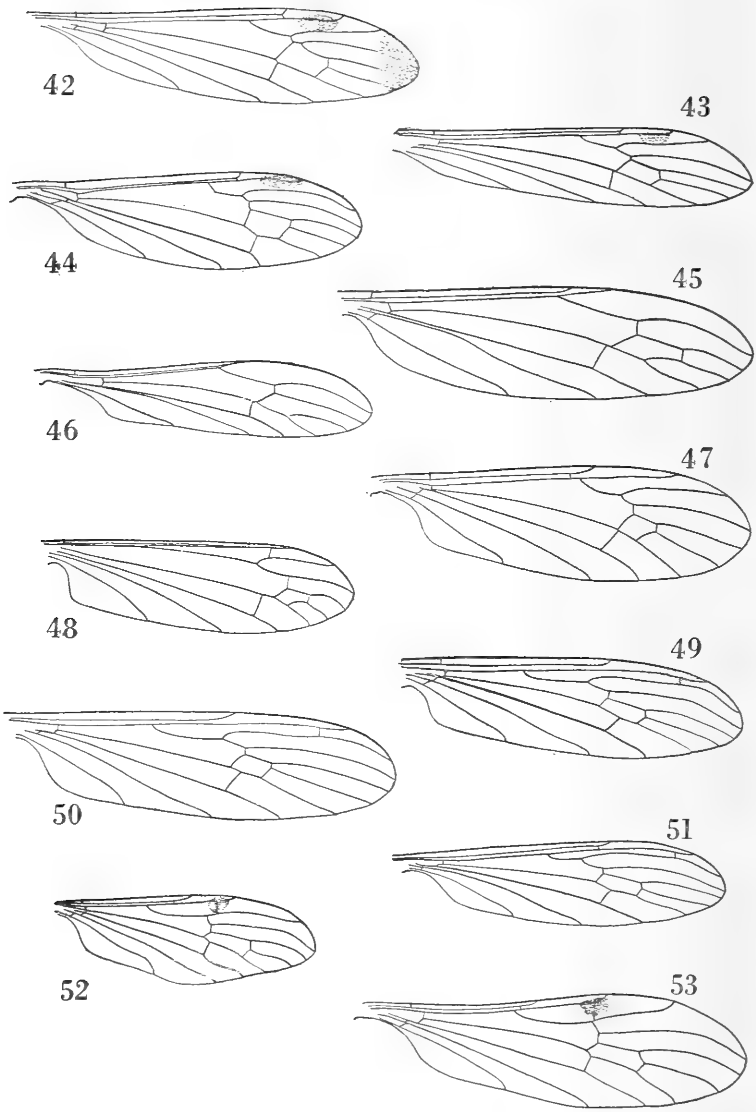


WINGS OF TIPULIDAE (LIMNOBIINI)

29, *Limnobia cinctipes*. 30, *L. parietina*. 31, *L. solitaria*. 32, *L. fallax*. 33, *L. indigena*. 34, *L. triocellata*. 35, *L. tristigma*

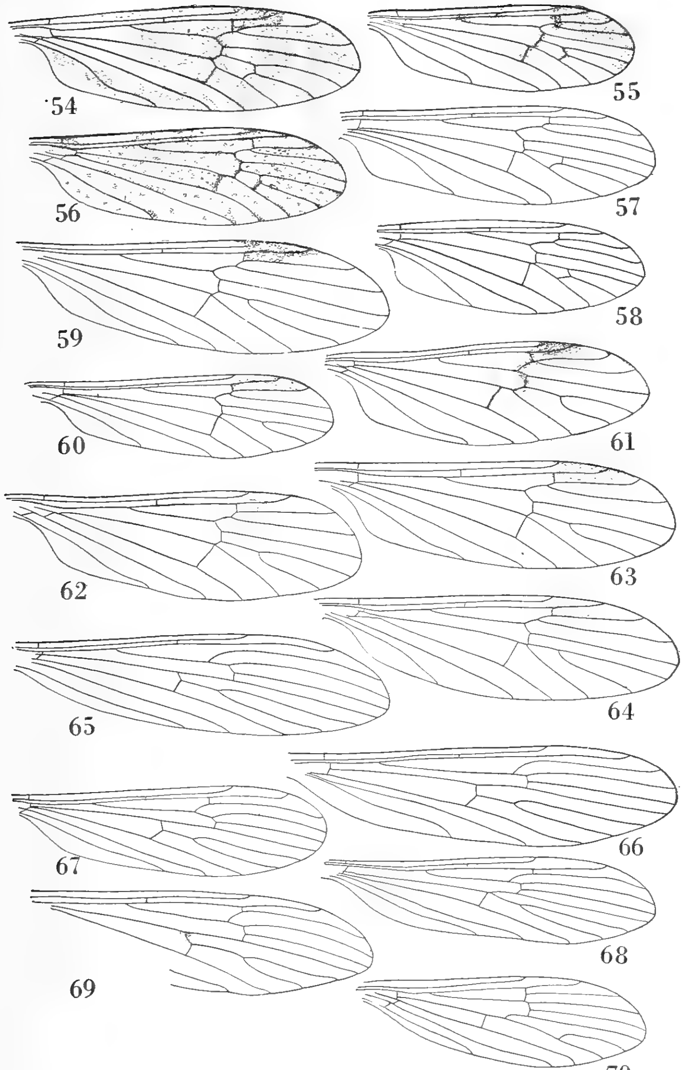
36, *Rhipidia maculata*. 37, *R. bryanti*. 38, *R. fidelis*. 39, *R. shannoni*. 40, *R. domestica*

41, *Discobola argus*



WINGS OF TIPULIDAE (ANTOCHINI)

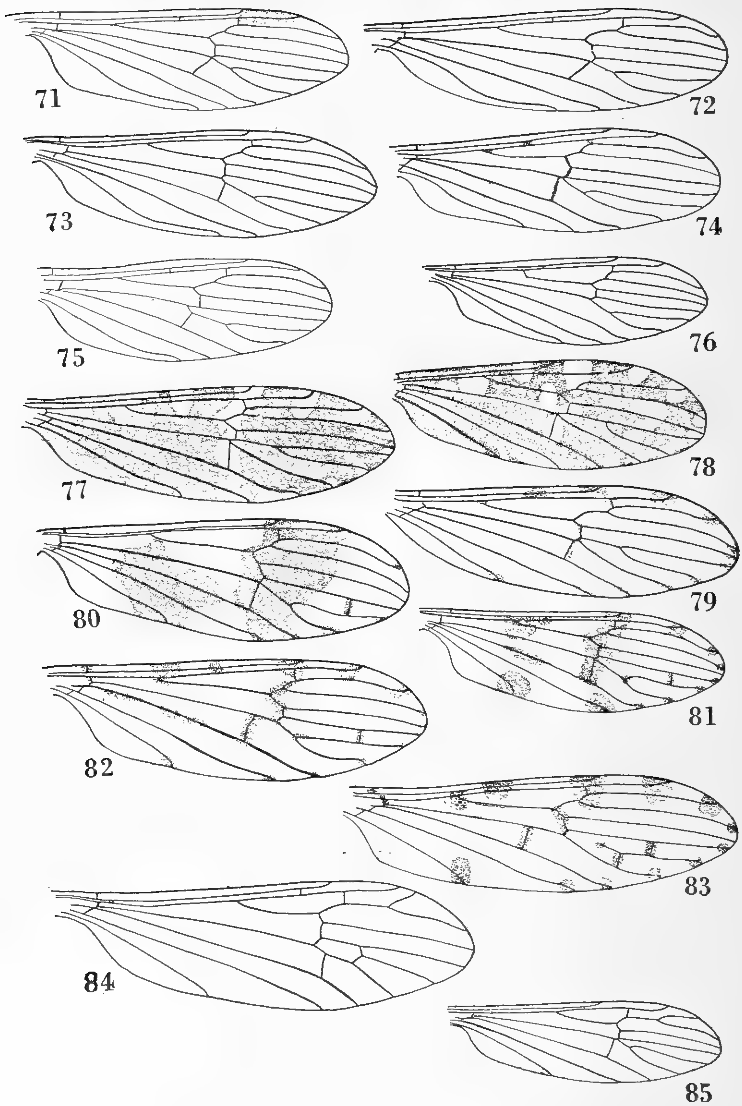
42, *Rhamphidia flavipes*; 43, *R. mainensis*. 44, *Elephantomyia westwoodi*. 45, *Toxorhina magna*; 46, *T. muliebris*. 47, *Atarba picticornis*. 48, *Antocha saxicola*. 49, *Dicranoptycha germana*; 50, *D. winnemana*; 51, *D. sobrina*. 52, *Teucholabis complexa*; 53, *T. lucida*



WINGS OF TIPULIDAE (ERIOPTERINI)

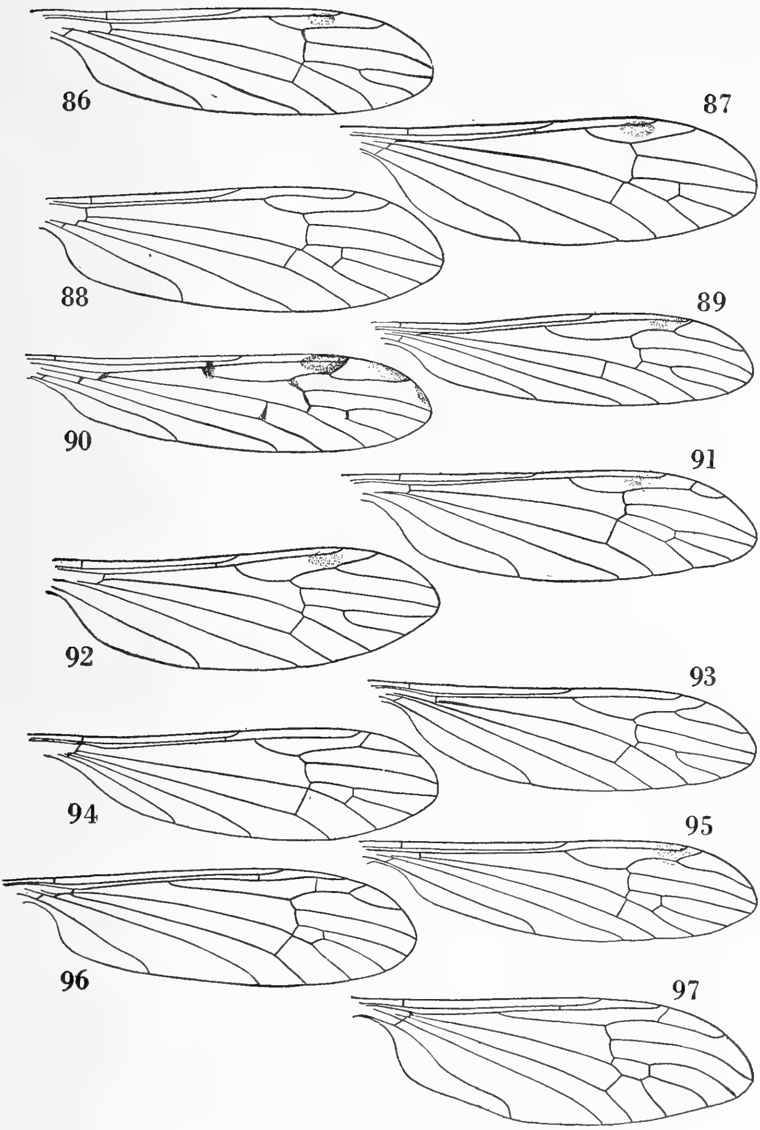
54, *Ormosia nubila*. 55, *O. apicalis*. 56, *O. innocens*. 57, *O. nigripila*. 58, *O. pygmaea*. 59, *O. nimbipennis*. 60, *O. rubella*. 61, *O. meigenii*. 62, *O. monticola*. 63, *O. mesocera*. 64, *O. megacera*

65, *Molophilus hirtipennis*. 66, *M. pubipennis*. 67, *M. fultonensis*. 68, *M. nova-caesariensis*. 69 *M. comatus*. 70, *M. ursinus*



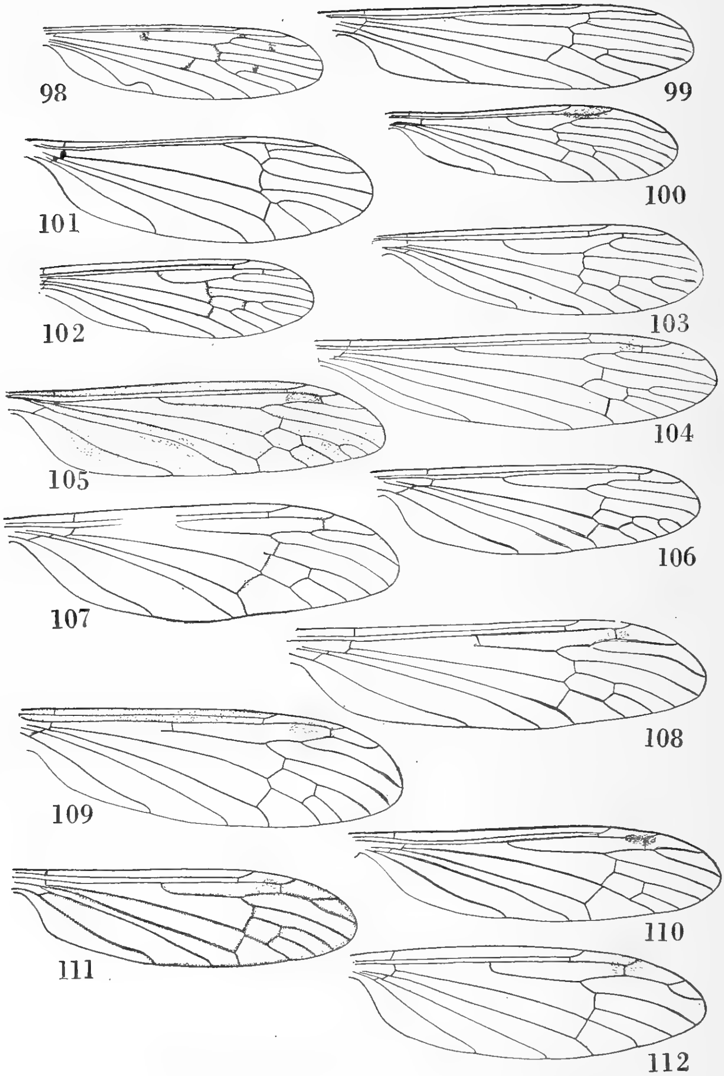
WINGS OF TIPULIDAE (ERIOPTERINI)

71, *Erioptera villosa.* 72, *E. septemtrionis.* 73, *E. vespertina.* 74, *E. chrysocoma.* 75, *E. chlorophylla.* 76, *E. straminea.* 77, *E. caloptera.* 78, *E. needhami.* 79, *E. parva.* 80, *E. venusta.* 81, *E. armillaris.* 82, *E. graphica.* 83, *E. armata.* 84, *E. nyctops.* 85, *E. stigmatica*



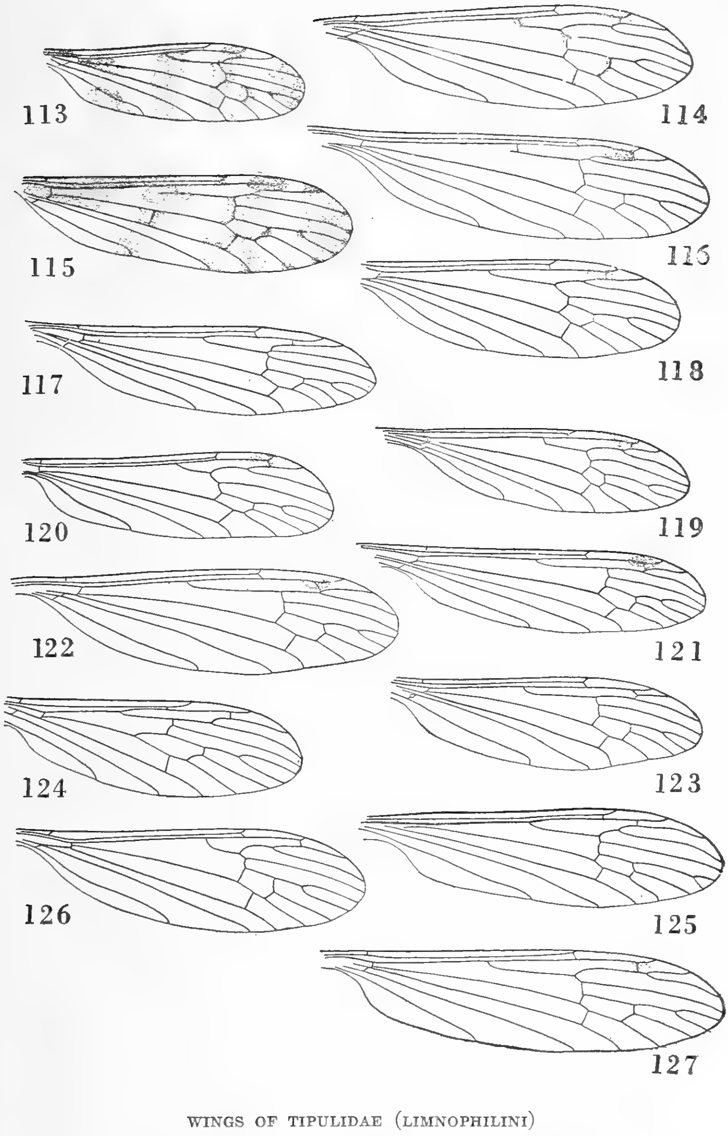
WINGS OF TIPULUDAE (ERIOPTERINI)

86, *Gonomyia alexanderi*. 87, *G. sacandaga*. 88, *G. manca*. 89, *G. mathesoni*. 90, *G. blanda*. 91, *G. sulphurella*. 92, *G. florens*. 93, *G. cognatella*. 94, *G. noveboracensis*. 95, *G. subcinerea*
96, *Rhabdomastix caudata*. 97, *R. flava*



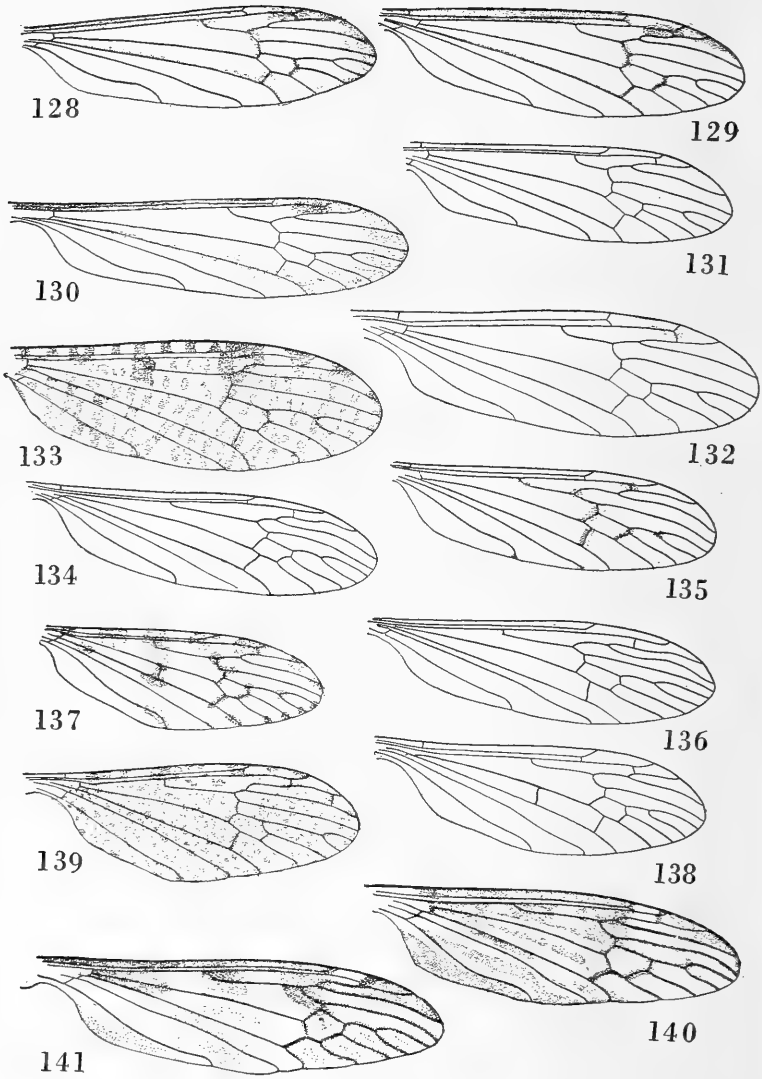
WINGS OF TIPULIDAE (ERIOPTERINI, HEXATOMINI)

98, *Helobia hybrida.* 99, *Trimicra anomala.* 100, *Gnophomyia tristissima.* 101, *Cryptolabis paradoxa.* 102, *Cladura flavoferruginea*; 103, *C. delicatula* 104, *Penthoptera albitarsis.* 105, *Eriocera spinosa*; 106, *E. brachycera*; 107, *E. longicornis*; 108, *E. cinerea*; 109, *E. wilsonii*; 110, *E. tristis*; 111, *E. fultonensis.* 112, *Hexatoma megacera*



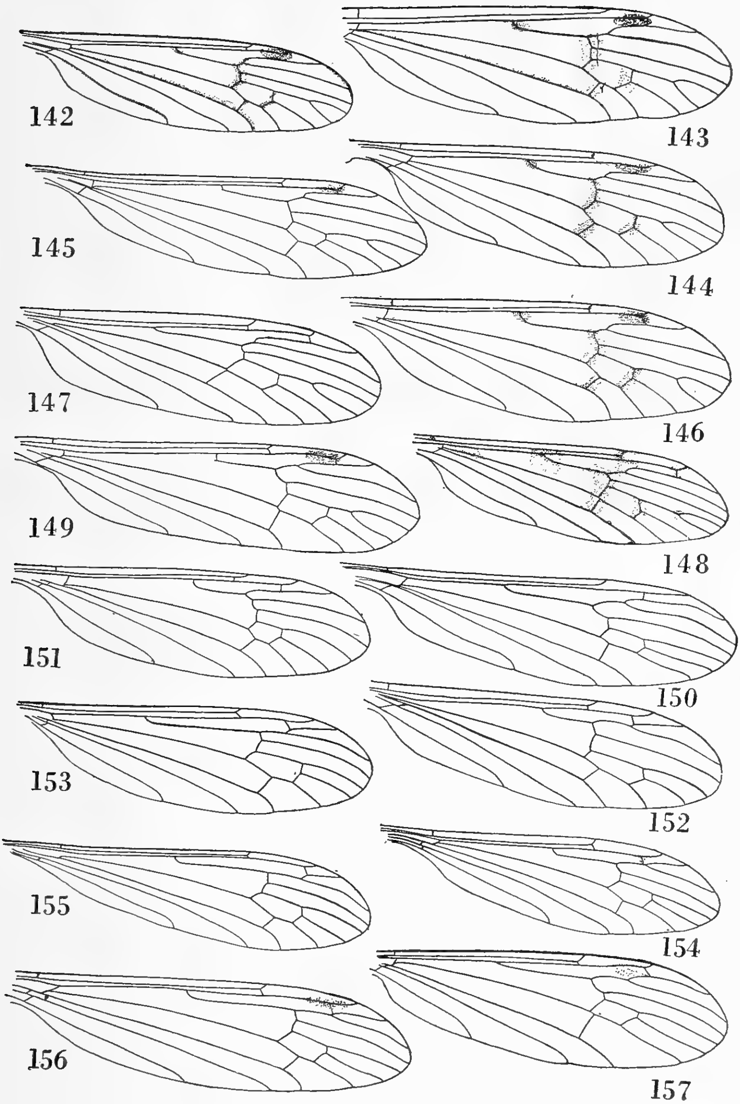
WINGS OF TIPULIDAE (LIMNOPHILINI)

113, *Limnophila macrocera*. 114, *L. unica*. 115, *L. fasciolata*. 116, *L. poetica*. 117, *L. tenuicornis*. 118, *L. niveitarsis*. 119, *L. albipes*. 120, *L. laricicola*. 121, *L. tenuipes*. 122, *L. imbecilla*. 123, *L. recondita*. 124, *L. areolata*. 125, *L. brevifurca*. 126, *L. toxoneura*. 127, *L. ultima*



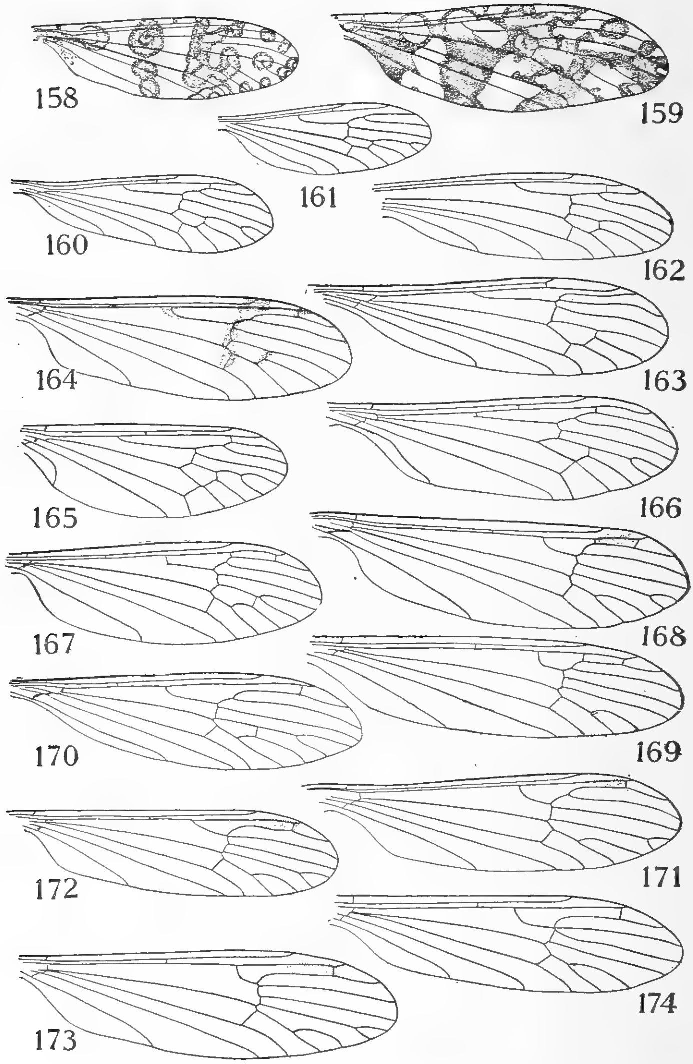
WINGS OF TIPULIDAE (LIMNOPHILINI)

128, *Limnophila adusta.* 129, *L. similis.* 130, *L. terrae-novae.* 131, *L. novae-angliae.* 132, *L. lutea.* 133, *L. irrorata.* 134, *L. inornata.* 135, *L. luteipennis.* 136, *L. nigripleura.* 137, *L. aprilina.* 138, *L. johnsoni.* 139, *L. fuscovaria.* 140, *L. alleni.* 141, *L. marchandi*



WINGS OF TIPULIDAE (LIMNOPHILINI)

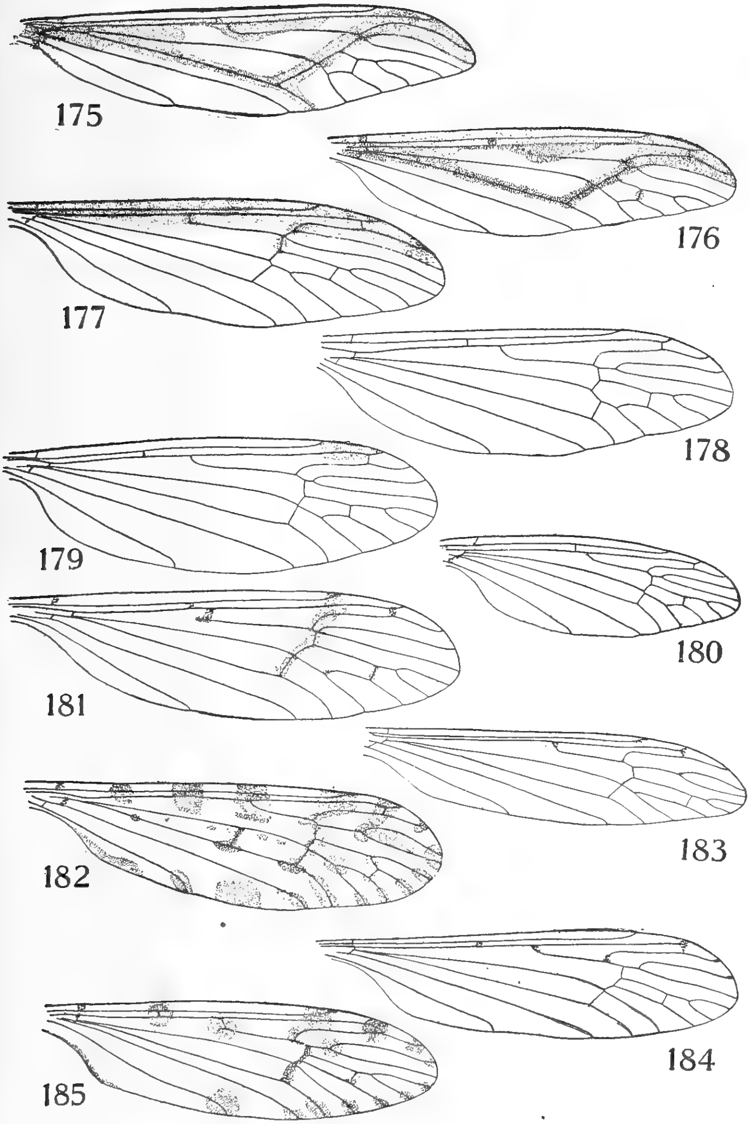
142, *Limnophila rufibasis*. 143, *L. simplex*. 144, *L. munda*. 145, *L. mundoides*. 146, *L. terebrans*. 147, *L. cubitalis*. 148, *L. montana*. 149, *L. subcostata*. 150, *L. noveboracensis*. 151, *L. emmelina*. 152, *L. lenta*. 153, *L. quadrata*. 154, *L. osborni*. 155, *L. stanwoodae*. 156, *L. edwardi*. 157, *L. sylvia*



WINGS OF TIPULIDAE (LIMNOPHILINI, PEDICIINI), AND TWO SPECIES IN RHYPHIDAE

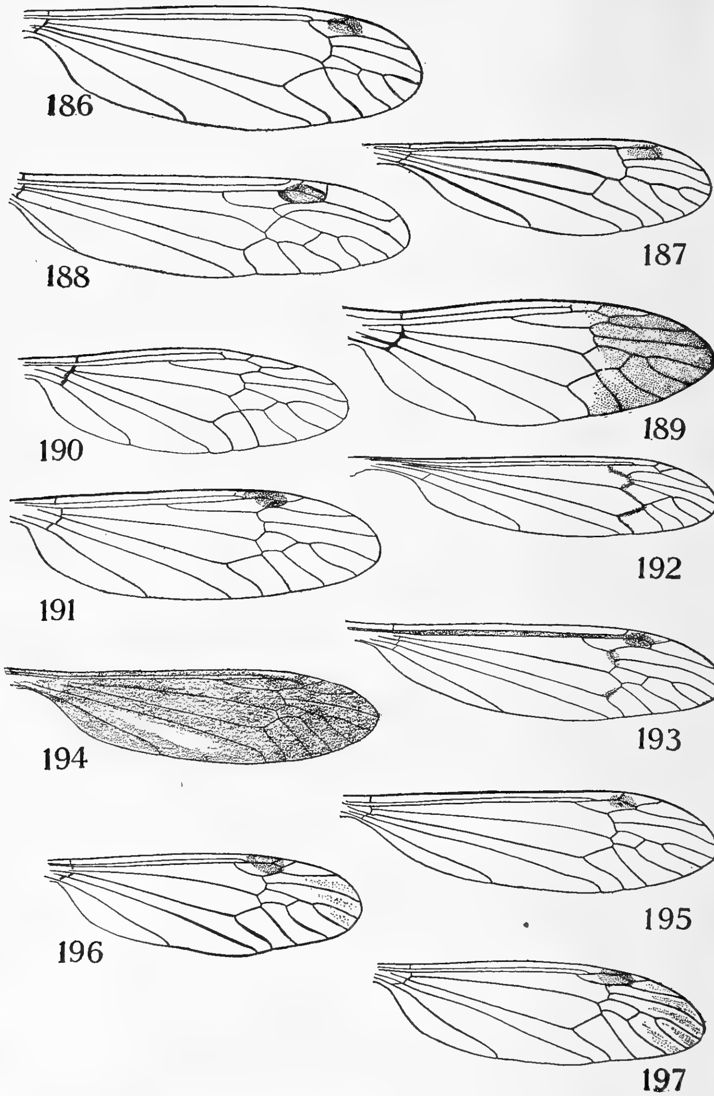
158, *Epiphragma fascipennis*; 159, *E. solatrix*. 160, *Adelphomyia americana*; 161, *A. minuta*; 162, *A. cayuga*. 163, *Ulomorpha pilosella*. 164, *Ula elegans* 165, *Trichocera brumalis*; 166, *T. subsinuata*

167, *Dicranota pallida*; 168, *D. noveboracensis*; 169, *D. rivularis*. 170, *Rhaphidolabis flaveola*; 171, *R. tenuipes*; 172, *R. rubescens*; 173, *R. cayuga*; 174, *R. modesta*



WINGS OF TIPULIDAE (PEDICIINI)

175, *Pedicia albivitta.* 176, *P. confermina*
177, *Tricyphona inconstans.* 178, *T. calcar.* 179, *T. autumnalis*, male; 180, *T. autumnalis*, female. 181, *T. auripennis.* 182, *T. hyperborea.* 183, *T. katahdin.* 184, *T. paludicola.* 185, *T. vernalis*

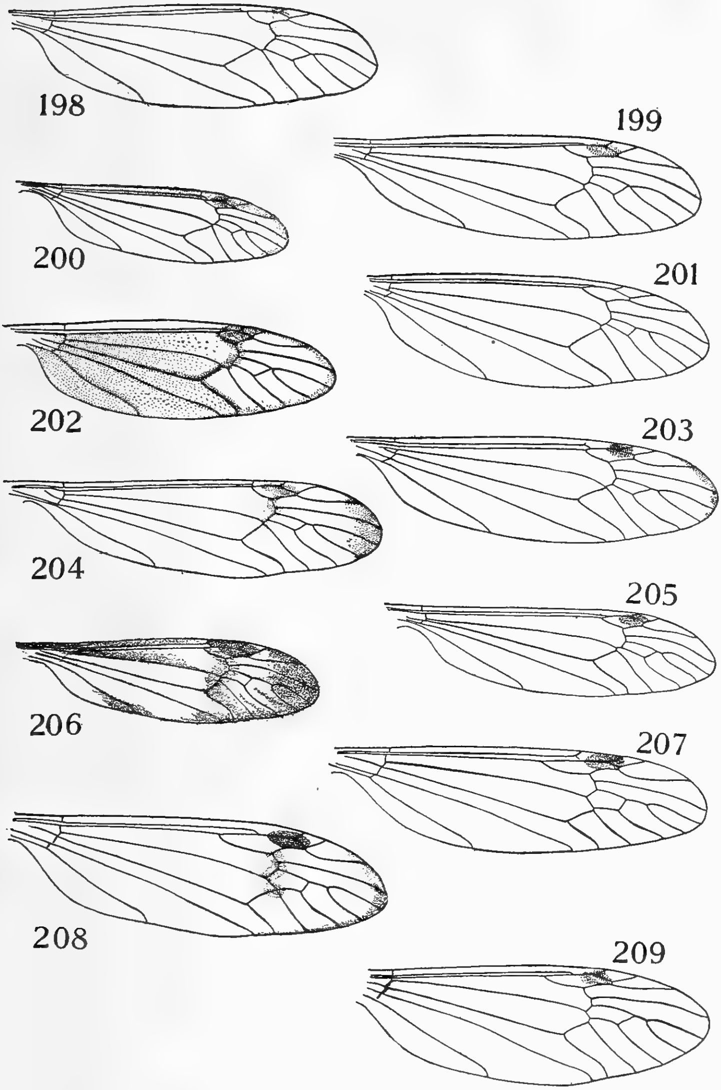


WINGS OF TIPULIDAE (DOLICHOPEZINI, CTENOPHORINI, TIPULINI)

186, *Oropeza obscura*. 187, *Dolichopeza americana*. 188, *Brachypremna dispellens*

189, *Ctenophora apicata*, normal form; 190, *C. apicata*, black form. 191, *Tanyptera frontalis*

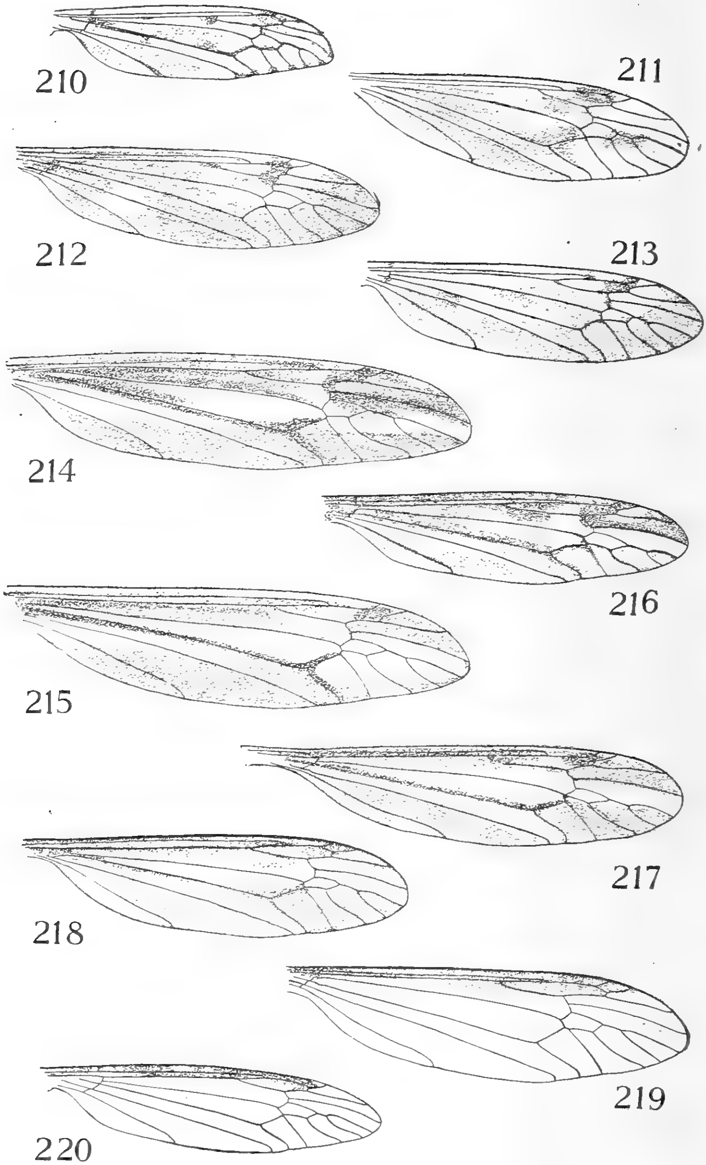
192, *Longurio testaceus*; 193, *L. minimus*. 194, *Stygeropis fuscipennis*. 195, *Tipula oropezoides*; 196, *T. unimaculata*; 197, *T. algonquin*



WINGS OF TIPULIDAE (TIPULINI)

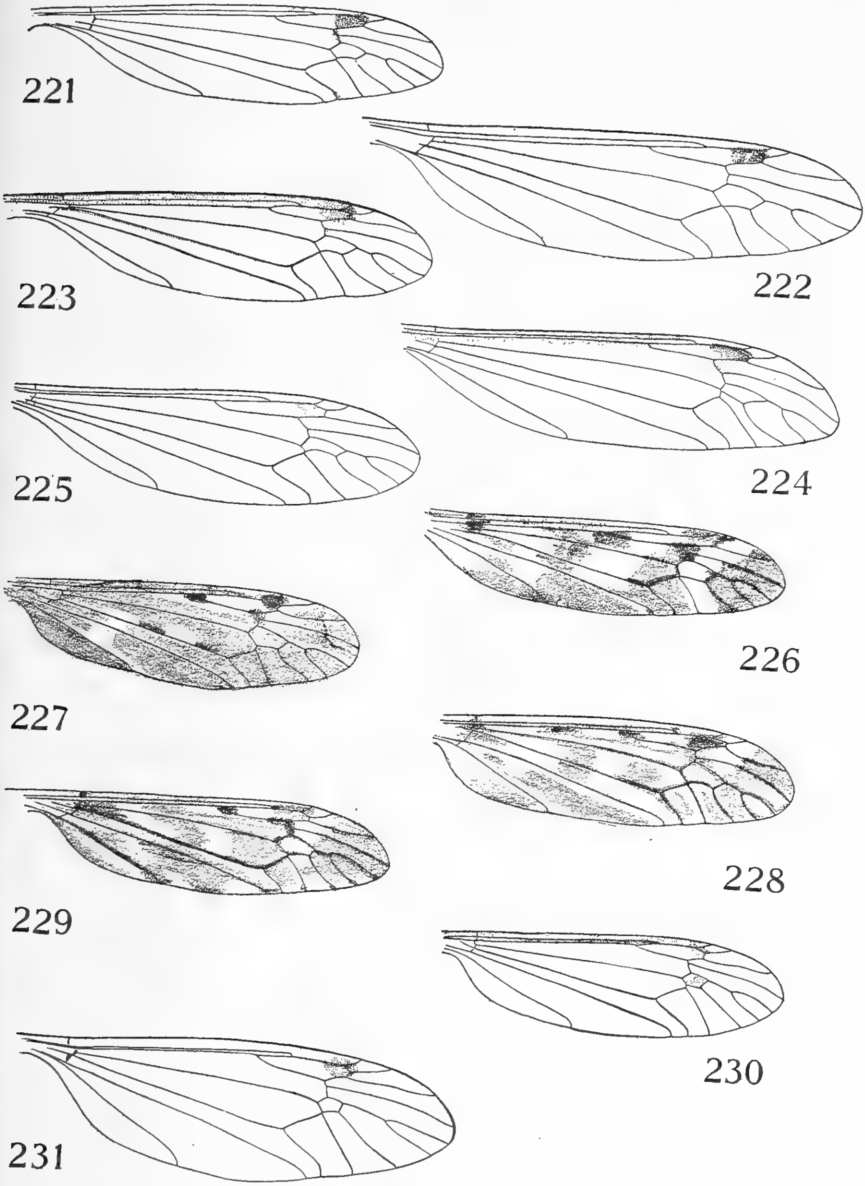
198, *Nephrotoma ferruginea*. 199, *N. tenuis*. 200, *N. macrocera*. 201, *N. xanthostigma*. 202, *N. lugens*. 203, *N. pedunculata*. 204, *N. incurva*. 205, *N. penumbra*

206, *Tipula unifasciata*. 207, *T. collaris*. 208, *T. nobilis*. 209, *T. pachyrhinoides*



WINGS OF TIPULIDAE (TIPULINI)

210, *Tipula abdominalis.* 211, *T. hermannia.* 212, *T. angustipennis.* 213, *T. senega.* 214, *T. caloptera.* 215, *T. strepens.* 216, *T. bella.* 217, *T. eluta.* 218, *T. tricolor.* 219, *T. sayi.* 220, *T. cunctans*



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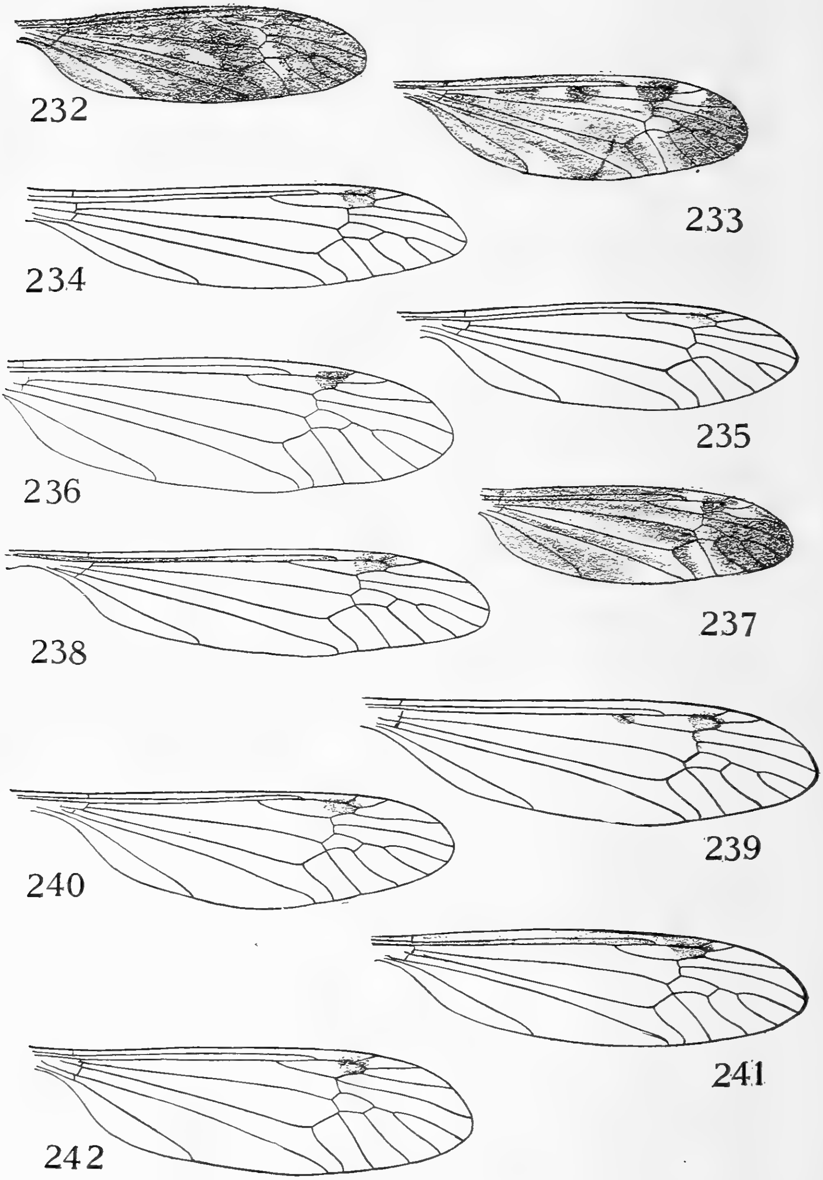

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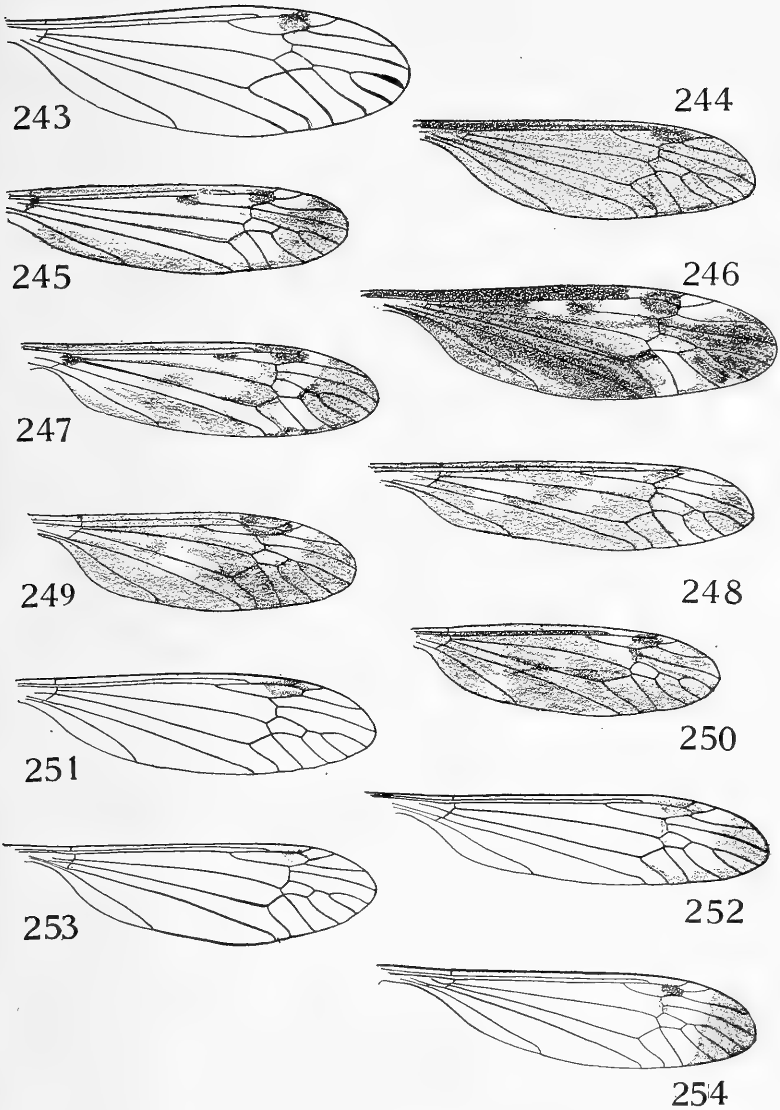

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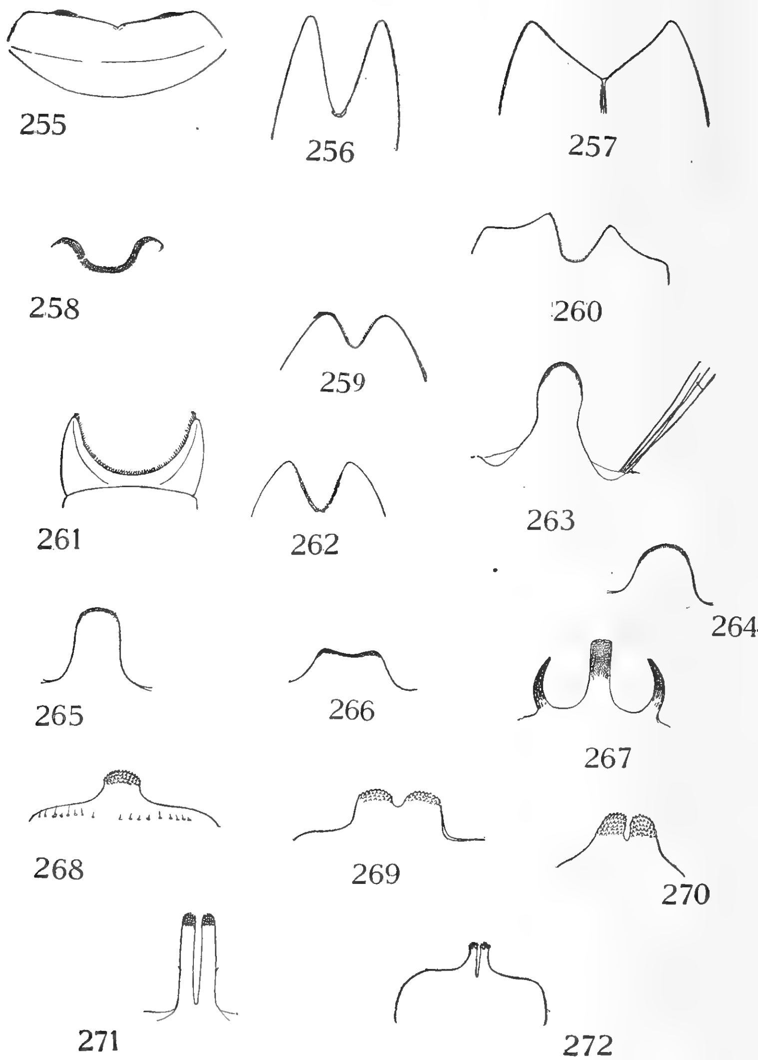

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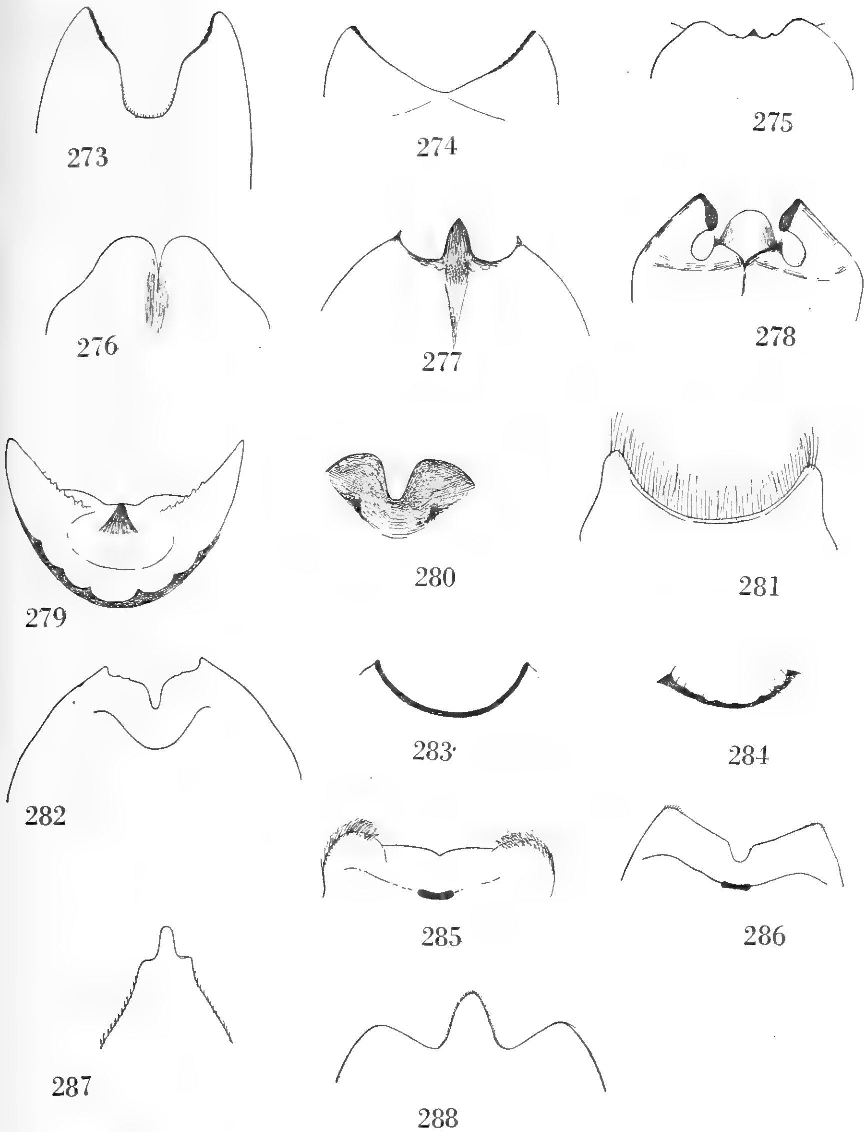

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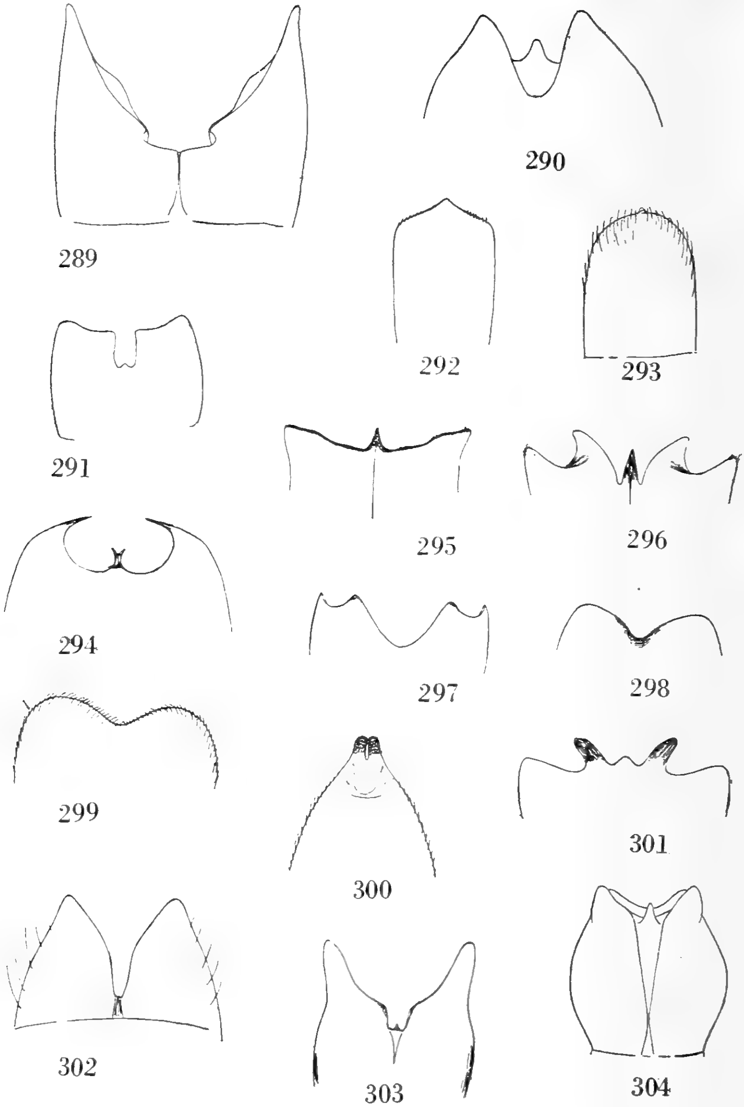

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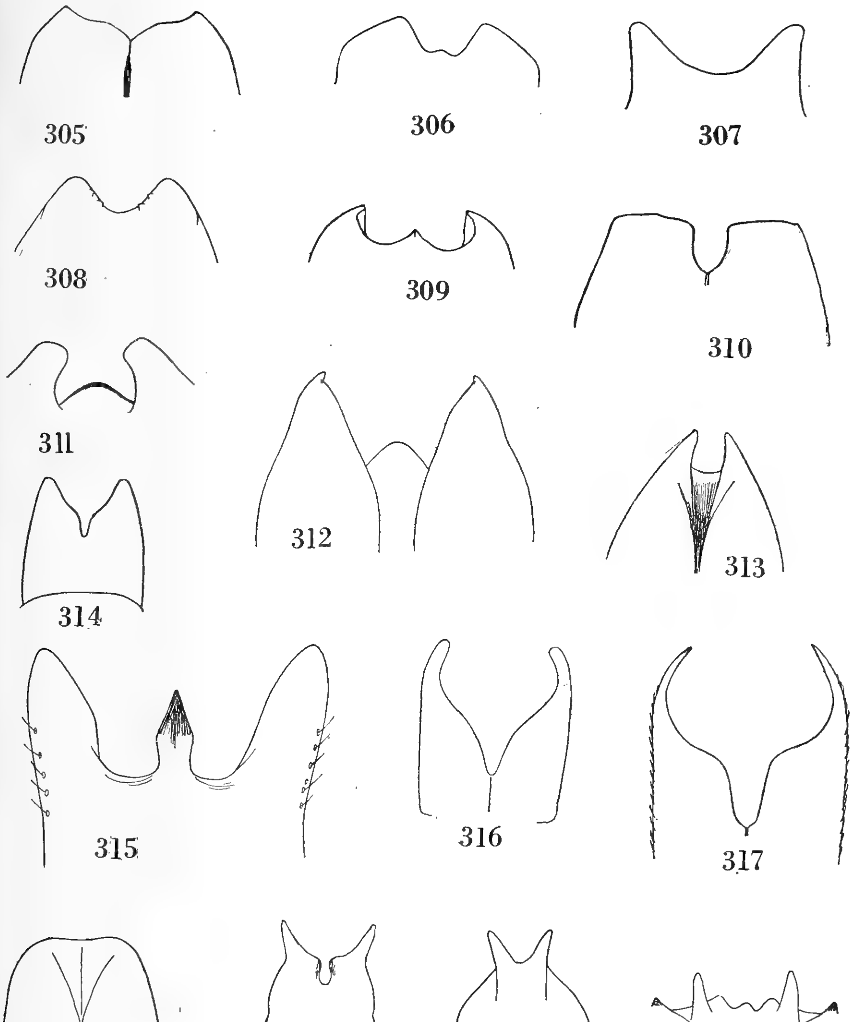

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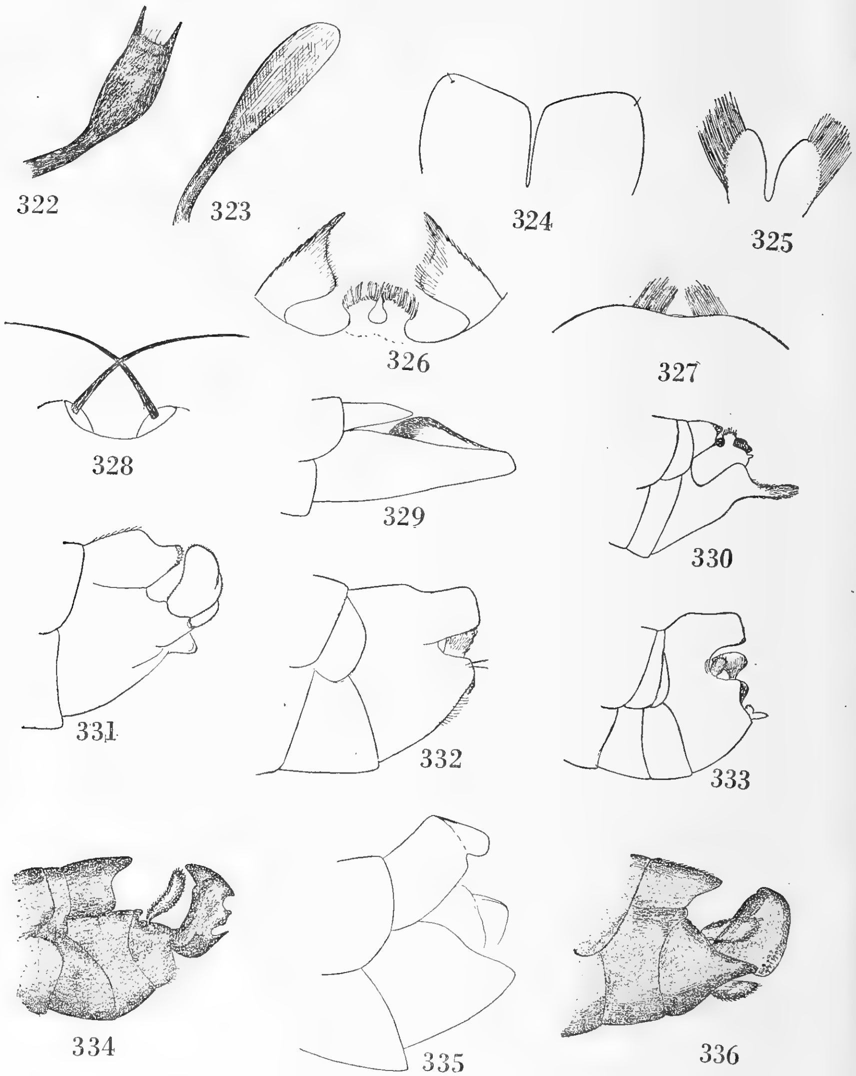

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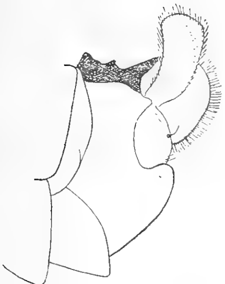
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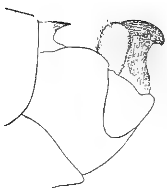
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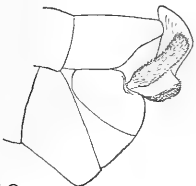
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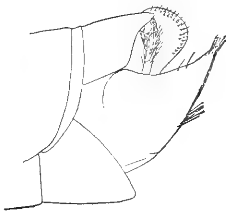
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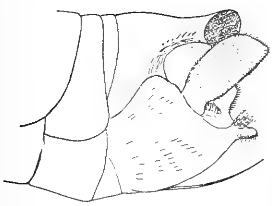
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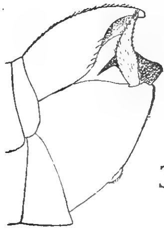
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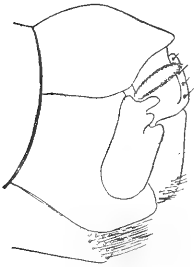
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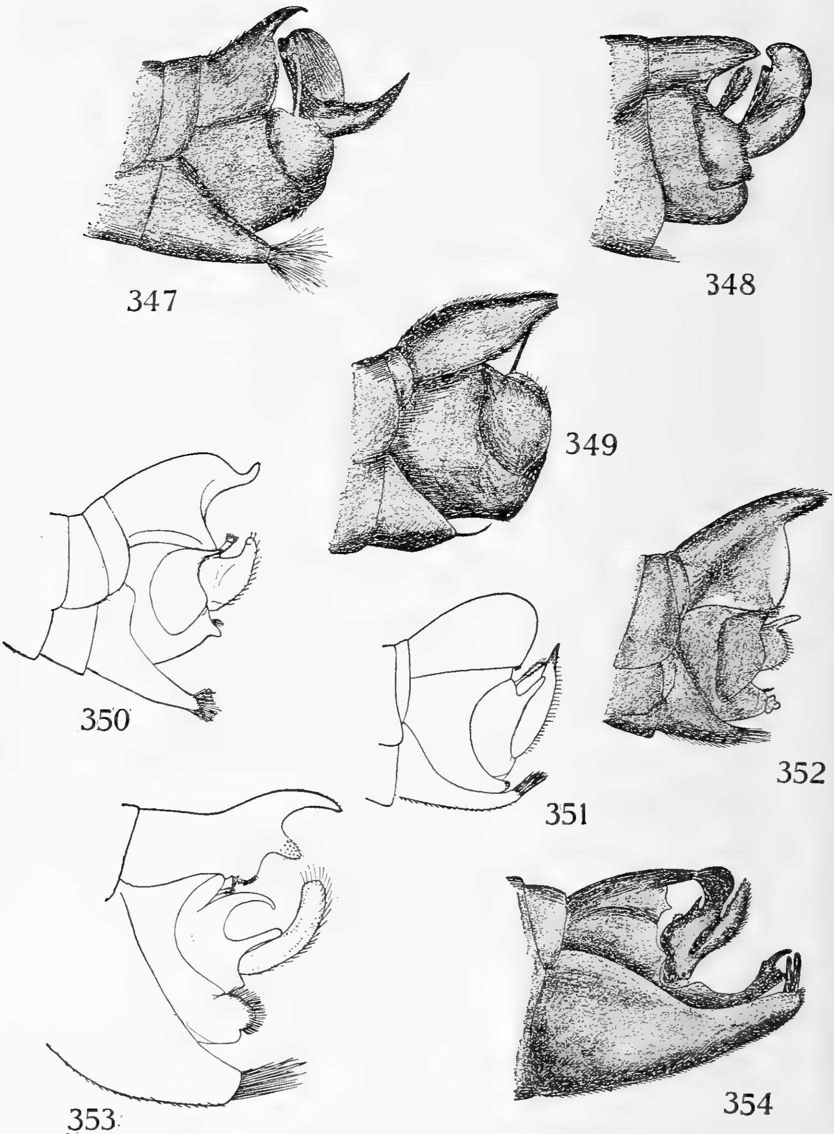

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JUNE, 1919 MEMOIR 27

CORNELL UNIVERSITY
AGRICULTURAL EXPERIMENT STATION

THE INFLUENCE OF LOW TEMPERATURE ON SOIL BACTERIA

A. F. VASS

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THE INFLUENCE OF LOW TEMPERATURE ON SOIL BACTERIA

A. F. Vass

Temperature is one of the most important factors influencing the growth and reproduction of microorganisms. Considerable work has been done in studying the effect of low temperature on the vitality and growth of bacteria, but the results have varied so greatly that it is difficult to draw any very definite conclusions from them. Certain investigators have found in frozen soils what they believed to be bacterial growth and reproduction to an even greater extent than is found at temperatures usually considered most favorable for protoplasmic activity.

The increased use of ice and the knowledge of water-borne epidemics have stimulated investigation in regard to the ability of the pathogenic bacteria to withstand freezing and storage in ice. In the work with pure cultures of pathogenic and nonpathogenic bacteria a great variation in results has been obtained. The natural ice dealer can find plenty of evidence to support his theory that the pathogenic bacteria in water are killed when the water is frozen and the ice stored for summer use. On the other hand, the public health officer can present equally strong evidence to show that the bacteria are not killed by freezing.

HISTORICAL

The literature herein reviewed deals with the ability of the pathogenic and the nonpathogenic bacteria to withstand exposure to low temperature, the influence of low temperature on the bacterial flora of the soil, and the cause of the death of the cell upon exposure to low temperature together with the factors that influence it.

PURE CULTURES

In the work with pure cultures both the pathogenic and the nonpathogenic forms were used. In some cases, however, there may be some doubt as to the purity of the cultures.

Regarding the resistance of bacteria to low temperatures, it was found by Schumacher (1874)[1], Göppert (1875), Frisch (cited by Pfeffer, 1903:238), Dewar and McHendrick (cited by Pfeffer, 1903:238), and Meyer (1900), that neither the spores nor the vegetative cells were killed by an exposure of several hours to temperatures ranging from −20° to −200° C.

Pictet and Yung (1884) exposed *Micrococcus lutea* and the vegetative cells of *Bacillus anthracis* to a temperature of −70° C. for one hundred and eight hours; this resulted in the death of the bacteria, as did also a temperature of −130° C. for twenty hours. The spores of *Bacillus subtilis*, *Bacillus anthracis*, and *Bacillus ulna* were not affected by the above-named temperatures. These results verified the conclusion of Melsens (1870), that long exposure of the yeast cells to −91° C. greatly decreases the fermentative activity. The enzyme of the yeast and the toxins of the poisonous bacteria were destroyed by exposure to extremely low temperatures. In his later work with microbes and diatoms, Pictet (1893) found that continued cold at −200° C. did not destroy these.

In studying the bacterial flora of snow, Janowski (1888) noted that continued low temperatures had very little effect on the bacteria. He found several hundred bacteria per cubic centimeter in water from snow.

Forster (1892) noted that the kinds of bacteria able to grow at 0° C. were not very numerous, but they seemed to be widely distributed, especially in water and on the surface and in the intestinal tract of both fresh- and salt-water fish.

In his work with *Bacillus anthracis*, Klepzoff (1895) noted that long exposure to low temperatures reduced the virulence of the organism and that the bacteria in blood and various organs were killed by exposing them to a temperature of −24° C. for twelve days. The colonies on agar plates were destroyed by exposing them for twenty-five days to the above-named temperature.

Kasansky (1899) exposed the pest bacillus and the diphtheria bacillus to temperatures ranging from −10° to −30° C. for five months and found that they were alive at the end of the experiment.

In their investigations with pure cultures of *Bacillus typhosus*, Sedgwick and Winslow (1900) found that from 30 to 60 per cent of the bacteria were destroyed during the first hour of freezing, and at the end of two weeks 99 per cent were destroyed. They studied the effect of alternate

[1] Dates in parenthesis refer to *Literature cited*, pages 1071 to 1074.

freezing and thawing, and noted that it was only slightly more harmful than continued freezing. Park (1901), in working with the same organism, found that all the bacteria were killed when embedded in ice for twenty-two weeks.

Macfadyen (1900) exposed bacteria to the temperature of liquefied air for twenty hours without its affecting their vital properties. The yeast-cell plasma also retained its peculiar properties to effect the production of carbon dioxide and alcohol. In a later report (1903) Macfadyen gives results from using liquid hydrogen, the temperature of this being −252° C. No appreciable effect on the bacteria was noted.

In studying the effect of the storage of ice on the bacteria contained therein, Sparks (1908) concluded that ice, even when cut from water which may contain pathogenic bacteria, is utterly incapable of passing on the disease if it is stored for some time before using. Similar results were obtained by Reudiger, who found that *Bacillus coli* was destroyed by storing in ice for eight weeks, and that the *Bacillus typhosus* organism was dead at the end of thirty-one days.

Budinov (1909) inoculated sterile milk with *Bacterium lactis acidi* and noted the effect of temperature on the life of the organism. At 30° C. most of the bacteria were dead in nine days, and at room temperature very few were alive at the end of eighteen days; while at 0° C. there was no change after thirty days. Alternate thawing and freezing had little or no effect. In such a case, however, temperature acts indirectly. The more favorable the temperature for growth, the greater is the production of acid, which in turn destroys the bacteria.

Poppe (1914) exposed the anthrax bacillus to a temperature of −16° C. for two weeks. The virulence and the reproductive capacity of the organism were not affected.

Jordan (1916) concluded that freezing had about the same effect as slow sand filtration, and that a great majority of the typhoid bacilli perish in a short time in ice, less than 1 per cent remaining alive after three weeks of freezing.

Hilliard, Torossian, and Stone (1915) noted, in their work with *Bacillus coli*, that 99 per cent of the organisms were killed by freezing in tap water for three hours; in the case of *Bacillus subtilis*, 80 per cent were killed under similar conditions. When the bacteria were placed in cream containing 30 per cent of butterfat, a protective action was noted.

Bartram (1916) exposed several of the disease-producing bacteria to winter temperatures for several months. Of the six cultures exposed, only two survived.

SOIL FLORA

Among the early workers who studied the influence of temperature on the bacterial flora of the soil may be mentioned Remy (1902), who studied the seasonal variations. His quantitative study showed no great variation in the different seasons. No samples were taken during the winter.

A correlation between the number of bacteria in the soil and the moisture content was noted by Hiltner and Störmer (1903). Their results indicated also that there was a decrease in the total number of bacteria as the temperature of the soil was lowered. They noted, however, that certain of the frozen samples gave rather high results. Fabricius and Von Feilitzen (1905) found the same correlation to exist between temperature and the bacteria count. Their tests were made during the growing season.

Engberding (1909) concluded, from his studies of bacterial activity in fallow and cropped, and manured and unmanured, plots, that the moisture content was more important than the temperature. Most of his samples were taken during the period of plant growth. Of the two frozen samples studied, the counts were not so high as in some of the unfrozen samples, but they were sufficiently high to show that there are large numbers of bacteria in frozen soil.

Conn (1910) made a careful study of the bacterial flora thruout the year. He concludes from his results that quantitative determinations by means of the gelatin-plate method show that bacteria may be present in the soil in large numbers during the winter, and that there seems to be a rapid multiplication of bacteria in frozen soil. He noted that the number of bacteria increased and decreased nearly parallel with the moisture content of the soil in the frozen samples, but during the winter there was a striking exception to this. In a continuation of the above work (Conn, 1912) his earlier findings were confirmed. The same marked increase in number of bacteria in frozen soil, and decrease in thawed soil, was noted. The increase during the winter was thought to be due to the actual multiplication of the bacteria rather than to a mere rise of the organisms from lower depths brought about by mechanical forces alone.

Conn attempted to divide the soil bacteria into three classes — rapid liquefiers, slow growers, and Actinomyces. He found the greatest increase in the group of slow growers when the soils were frozen. In the quantitative work in the pure cultures he noted that certain types of soil bacteria occur thruout the year, while others apparently exist for short periods only and tend to recur at other times under similar conditions. He suggested the possibility that a different class of bacteria is in the ascendancy in winter from those which are benefited by the warm weather of summer; in which case the increase is not due directly to the low temperature, but to the depressing effect of the cold upon the group of bacteria which is able in summer to keep the winter bacteria in check.

Hutchinson (1911–12) noted that biological changes in the soil take place at a greater rate in the soils of India than in the European soils. The temperature of the India soils ranges from 25° to 30° C. during the growing season, whereas that of the European soils ranges from 16° to 18° C. At the lower temperatures ammonification and nitrification go on at the same rate, but in the soils of India there tends to be an accumulation of ammonia due to the increased activities of the ammonifying bacteria at the higher temperature.

The work of Conn was continued by Brown and Smith (1912) in their investigations of the bacterial activities of frozen soils. They made quantitative determinations of the number of bacteria in the soil during the fall, winter, and spring seasons. They noted a gradual decrease in the number of bacteria as the temperature was lowered. This decrease continued with more or less variation until March 1, when there was a marked increase. They suggested that their results confirm Conn's conclusion that bacteria are alive and multiply in frozen soils. They studied what they called the ammonifying, nitrifying, denitrifying, and nitrogen-fixing powers of frozen soils. These tests were made by inoculating 100 grams of an air-dry soil with a soil infusion representing five grams of the frozen soil to be treated. The nitrogenous materials added were stirred into the unsterilized soil by means of sterile spatulas. The authors conclude that frozen soils possess a much greater ammonifying power than do non-frozen soils, and that the ammonifying power of the soil increases until the temperature almost reaches zero, when a decrease occurs, and this is followed by a gradual increase which continues until the ammonifying power reaches its maximum at the end of the frozen period.

The nitrifying power of the frozen soils was weak and the ammonifying power was strong. The nitrogen-fixing power increased with the continuance of the frozen period, being independent of moderate changes in moisture conditions. In the fall the nitrogen-fixing power of the soil increased until the soil became frozen, when it almost ceased, after which a lesser nitrogen-fixing power was established.

Brown and Smith advanced the theory, which Conn suggested in an earlier publication, that the hygroscopic water in soils, remaining uncongealed, may serve as favorable media in which the bacteria may live and multiply to a comparatively large extent.

Czermak (1912) studied the changes in the so-called physical properties of soils resulting from their subjection to low temperature, high temperature, and the action of salts. He noted that when the soil colloids were coagulated by freezing, the soil surface and the hygroscopicity were reduced, and part of the nitrogen in the soil solution was absorbed, thus reducing the amount of available nitrogen. Alternate freezing and thawing increased the coagulation of the soil colloids. The length of time was more important than the intensity of the freeze. Hoffmann (1914), however, found little or no variation in the surface area of soils due to freezing.

Lyon and Bizzell (1913) studied the effect of freezing on the nitrifying power of the soil. They noted that freezing produced a soil favorable for nitrate formation. This was attributed to the beneficial effect of low temperature in overcoming the depressing influence of the crop previously grown.

Russell and Hutchinson (1913) offer an explanation very similar to Conn's to account for the increase of bacteria in frozen soils. They suggest that the protozoa may be the hostile organisms holding the bacteria in check in the unfrozen soils.

Conn (1914) verified in later studies what he had previously found, that the increase in bacteria in frozen soils is not due to the increase in moisture content which usually occurs in winter, and that the same increase may take place in potted soils where there is no possibility of the bacteria being carried up mechanically from lower depths during the process of freezing. He suggested the possibility that the increase may not be an actual multiplication but may result from the breaking up of the masses of bacteria by freezing. He considers this to be extremely

unlikely, however, for if such was the case the count following the thawing of the ground in the spring would not be so nearly the same as it was before the freeze. He attempted to explain this increase as due to a summer and winter flora but was unable to do so. There was a surprising similarity between the predominating types of bacteria found in different soils and in the same soil at different seasons.

In an attempt to explain the presence of large numbers of bacteria in frozen soils, Harder (1916) studied the effect of heavy frosts. He found that the number of bacteria in surface soil increased markedly after heavy frosts and maintained this high average during the winter months. Contrary to the findings of Conn and of Brown and Smith, Harder noted that the increase was directly related to the moisture content. His findings verified Conn's conclusion that the bacterial flora was more or less the same thruout the year, with the exception that after heavy frosts there was an increase in the proportion of small transparent colonies. Potted soils did not show this increase even when enriched with sugars. In fact the enriched soils showed fewer organisms in the frozen than in the unfrozen samples. Harder concludes that the increase in numbers was due to mechanical transportation by moisture coming up from below during heavy frosts.

Conn (1918), in his microscopic study of bacteria and soil fungi, found that there was more or less clumping of the bacteria on the soil particles, and in certain cases the organisms occurred in large sheets one individual thick. In practically all cases there was an increase in the individual count over the group count. In one table Conn gives the results of thirty-four groups and individual counts of soils made at different periods following the addition of manure. The results show that the individual count gives an increase of 50 per cent over the group count.

The findings of Brew and Dotterrer (1917) in their study of milk were very similar to those of Conn. Brew and Dotterrer noted a higher count with the microscope than with the plate method. The difference they attributed to the clumps of bacteria that do not break up on plating.

MILK FLORA

Stiles and Pennington (1909), in their investigation with ice cream, found that the samples showed what seemed to be an increase in the bacteria count for a few days, followed by a decrease on the fourteenth

day. This was followed by a more rapid increase until the highest point was reached on the twenty-seventh day. On the thirty-fourth day the counts were about equal to those on the fourteenth day.

Hammer (1912) concludes from his studies with stored ice cream that there is no increase in the number of bacteria during storage, as judged by the number of organisms developing on agar with an incubation temperature of 37° C. He assumes, of course, that the product is kept properly hardened.

Gordon, Prescott, Heinemann, and Pease (1914) noted a marked increase in the bacteria counts of fresh ice cream over the counts of the mix as it entered the freezer.

Esten and Mason (1915) concluded from their investigations that when ice cream is kept frozen for periods of at least a month, there is no marked increase or decrease in the bacteria count as shown by litmus lactose gelatin plate counts.

Ellenberger (1919) noted an increase due to the freezing process, which he thinks may be accounted for by the breaking-up of the clumps of organisms by the beating received from the dasher during freezing. He observed no radical change in the total number of bacteria in ice cream during storage. The groups of bacteria in ice cream as determined by litmus gelatin plates and litmus milk tubes did not change noticeably during storage.

CAUSE OF DEATH OF THE CELL

Several theories have been suggested to explain the specific action which results in the death of the plant cells when exposed to low temperatures. Du Hamel and Duffon (1737) advanced the theory that death was due to the bursting of the cell wall as a result of the expansion accompanying ice formation. Senebier (cited by Göppert, 1830) also supported this view, which was later disproved by Sachs (1860) and Nägeli (1861). The formation of ice crystals within the cell and in the intercellular spaces was noted by Göppert (1830), but in no case could he find ruptured cells. He considered death a result of freezing, and as being in no way affected by the rate of thaw. Sachs concluded from his results that the degree of killing of plants at a given temperature depended on the rate of thaw.

Müller-Thurgau (1880) and Molisch (1897) were unable to detect any great difference in the amount of killing due to the difference in rate

of thaw, except in a few specific cases. They believed that death was due to the rapid withdrawal of water from the cell to form the ice crystals in the intercellular spaces during the process of freezing, and that only when freezing took place very rapidly were ice crystals formed within the cell. Unfavorable conditions appear in general to reduce the power of resistance to cold, and a deficiency or excess of water or plant food would act in the same way.

Klemm (1895) noted that the visible changes and deformations produced in the protoplasm were due to sudden changes in temperature, and were not present when the cells were subjected to gradual changes.

D'Arsonval (1901) noted that yeasts and bacteria did not lose their vital properties when placed in liquid air for weeks. He thinks the fluid in the cell is probably not solidified if the cell is not ruptured, owing to the enormous osmotic pressure in those small organisms, for if their osmotic tension is lowered by placing them in a solution of sodium chloride, potassium chloride, or glycerin, they are readily killed. He suggests the possibility of determining the osmotic pressure of any given cell by the temperature at which its vitality is destroyed.

Matruchot and Molliard (1901) subjected plants to freezing, to drying, and to the action of solutions of high osmotic concentration. They observed a marked parallelism between the action of freezing and that of drying, and they concur with Molisch in that the death of the cell is due to a rapid drying-out of the tissues.

Mez (1905) noted, in his studies of the effect of supercooling on plant tissue, that where the ice formation began at once on reaching the freezing point the killing was not so great as where there was supercooling, and the formation of ice crystals took place rapidly. He thinks that when a temperature of −6° C. is reached, all solutions will crystallize out. The heat liberated by the crystallizing of the solutions and the formation of ice, will, after the cells are insulated by the ice mass, aid in keeping the temperature of the cell above that of the surrounding material. Mez holds that death is due to the direct effect of the cold.

Gorke (1907) noted that when the cell sap was frozen, certain proteids were precipitated, and that those plants that are most easily killed by freezing have their proteids precipitated at the highest temperatures. By using solutions of albumin to which had been added zinc sulfate, he was able to show that the concentration of the salts had a marked effect

on the precipitation of the proteids when the solutions were frozen. He assumed that killing from cold may be due to the precipitation of the proteids resulting from the concentration of salts in the sap as the water is removed to form the ice crystals within the intercellular spaces.

Heckel (1909) noted that anesthetics and freezing liberated coumarin very rapidly from certain plants, and that the characteristic odor was apparent from green plants in a few moments after freezing, whereas ordinarily it is not apparent until after the plants have become more or less dried. This seemed to indicate that freezing and drying affected the plant in much the same way.

In studying the relation between the density of cell saps and the freezing points of leaves, Ohlweiler (1912) noted that the extreme differences in sap density are generally accompanied by corresponding resistance to freezing. He found that when the cell structure was essentially the same, the density of the cell sap of the species would indicate its relative hardness.

Lepeschkin (1912) concludes that death in plant cells is preceded by a decomposition of the less stable protein compounds and later their coagulation. Capillary forces may play an important part in their coagulation, which in turn sets free energy that leads to the breaking down of the weaker compounds.

Maximow (1914), in his very excellent work in freezing sections of plants in solutions of various strengths of both organic and inorganic substances, found a remarkable protection to be exerted whenever the eutectic point of the substances did not lie too near the freezing point and whenever the substance was not exceedingly toxic. When the sections were immersed in these solutions and immediately frozen, as much protection was noted as when they were permitted to remain in the solution for several hours. The protective action was not in direct proportion to the osmotic pressure and the lowering of the freezing point, for it was considerably more rapid than the latter changes. Since the protective action did not depend on the time the plant was in the solution nor on the permeability of the protoplasm, Maximow concluded that the action is on the outer layer of the protoplasm, and that the withdrawal of water seems to be limited to the plasma membrane.

Chandler (1913) was able to reduce the killing temperature of plant tissue by increasing the sap density of the tissue. In the case of unripe

apples and pears, there was no indication that the rate of thawing had anything to do with the amount of killing at a given temperature.

SCOPE OF THE PRESENT INVESTIGATION

With the results of the aforesaid workers in mind, the author undertook the investigations herein reported in an attempt to answer the following questions: (1) Is there an actual growth and reproduction of the bacteria in frozen soils or solutions? (2) What is the effect of low temperature on *Bacillus radicicola* in solution, sand, and soil cultures? (3) To what is the protective action noted in solution and soil cultures due? (4) Why have so many investigators obtained such divergent results in their work with bacteria at low temperatures?

The widely varying results obtained by Conn, by Brown and Smith, and by Harder, would seem to indicate that the number of bacteria occurring in frozen soils as determined by the agar-plate method is due not to an actual multiplication of the bacteria but to some unknown condition. The findings of Harder would indicate that the moisture content is of prime importance, whereas Brown and Smith did not consider it so important. Conn found that potted soils showed the same marked increase as the field soils. Harder was unable to show this increase in the potted soils, and concluded that the bacteria were carried up from the lower depths by heavy frosts.

It is contrary to the general conception of plant and animal life to hold that bacteria will grow and multiply more rapidly at temperatures below zero than at the so-called favorable temperatures. The work of Conn, of Brown and Smith, and of Harder, gives little or no evidence to show that the bacteria do actually multiply in frozen soils, for the increase in bacteria counts noted by these investigators was based on the colonies appearing on the agar plates, and, as is well known, this method is in many cases a poor indicator of the actual number of bacteria present. The method is perhaps of value in a comparative way when comparing substances that have received more or less of the same treatment, but it seems very doubtful whether it has any real value when comparing normal and frozen soils. The results obtained by Brown and Smith are very good examples of this.

If there is not an actual increase in the number of bacteria in frozen soils — and it does not seem probable that there is — the large number of

colonies appearing on agar plates must be accounted for in some other way. As each colony on a plate may result from a single cell or from a cluster of many cells, it would seem that the increase obtained from frozen soils might be due to the breaking up of the masses of bacteria, not to an actual reproduction.

Both Conn and Harder considered this breaking-up process to be extremely unlikely, for if such was the case the count immediately after the thaw would not be so nearly the same as it was before the freeze. This objection, however, might not hold in the case of the bacteria, for they often grow in a jelly-like mass which might be ruptured by freezing but which if allowed to thaw gradually, as it would in the soil under a normal condition, might assume its original position. If such was not the case, one might expect more bacteria in recently thawed soil than in unfrozen soil. If the increase was due to a summer and a winter flora, as suggested by Conn, there should not be a rapid decrease in number of bacteria immediately after the thaw, for the soil would maintain for several days a temperature more favorable for the winter than for the summer flora. The soils that were allowed to thaw gradually in the field showed approximately the same number of bacteria as was shown by the soils before they were frozen, whereas the soils that were thawed rapidly in the laboratory showed a higher count. This would seem to indicate that the rate of thaw might be an important factor. The experiments reported herein were conducted with these considerations in mind.

METHODS OF INVESTIGATION

ORGANISMS

In the experiments dealing with the field soils, the bacterial flora of the soil was studied as it was observed on examination. A study was made of the different groups, but no marked correlation was noted between certain groups and the treatment of the soil. *Bacillus radicicola* from field pea was used for all the pure-culture work. This organism was selected because of its economical importance and habits of growth. It is easy to grow and identify, and is classed as a non-spore-bearing form. The latter character is of importance in low-temperature studies.

MEDIA

The organisms were grown in soil, sand, and solution cultures. The medium used for making the plate counts of the field soils was Conn's (1914)

asparaginate agar. The agar used in plating the *Bacillus radicicola* organism was the same as Wilson (1917) used in his studies. In the nutrient solutions the saccharose was replaced by mannite, 1 gram to a liter.

METHOD OF FREEZING, THAWING, AND PLATING THE BACTERIA

In the case of the field soils, the samples were collected in the field under sterile conditions and 20-gram portions were placed in sterile liter flasks. The samples were then taken to the laboratory in a frozen condition and treated immediately, water at the different temperatures being used to thaw the samples. Plates were poured from the 20,000 and 200,000 dilutions. Five plates were poured from each dilution in all cases. Ice and salt, liquid air, and outside temperatures, were used to freeze the laboratory samples.

The *Bacillus radicicola* organism was grown in sterile sand, soil, and water cultures. In the case of the sand and soil cultures 1-gram portions were weighed out into small, sterile, test tubes under sterile conditions, and subjected to the various treatments. The samples subjected to the liquid-air treatment were lowered into the wide-mouth Dewar bulbs containing the liquid air. Care was necessary to prevent bursting of the tube in freezing. The plates were incubated at 30° C. and counts were made at the end of four and seven days. Five plates from each of three dilutions were poured from all samples.

EFFECT OF RATE OF THAW ON BACTERIA COUNT

SOILS FROZEN IN THE FIELD

It would seem that if the large number of bacteria in frozen soils as shown by the plate method is due to the breaking up of the clusters of organisms, the rate of thaw should have some effect. In order to test this point, samples of Dunkirk clay soil containing 33 per cent of moisture were taken from the field in a frozen condition and thoroly mixed, and 20-gram portions were put into liter flasks. These samples were brought to the laboratory and plated by the dilution method. The only difference in the treatment was the temperature of the water blanks used in making the dilutions. The results are shown in table 1.

From the results shown in table 1, the rate of thaw seemed to have a marked effect as shown by the counts on agar plates. The increased count due to the sudden thawing of the soil with water at 30° C. was 200

per cent above that of the count made using water at 1° C. When the soil was allowed to thaw in the air the difference was less marked. It is interesting to note that when the temperature of the water used in plating the soil was raised to 40° C. there was always a drop in the counts. This may have been due to the death of the bacteria caused by the sudden change to higher or lower temperature. It seems more probable, however, that the higher temperatures may cause a greater or less coagulation of the masses, resulting in fewer colonies on the plates.

TABLE 1. EFFECT OF RATE OF THAW ON THE BACTERIA COUNT IN FIELD SOILS

Sample	Treatment	Bacteria per gram of dry soil
1	Water added at 1° C	3,100,000
2	Water added at 10° C	5,200,000
3	Water added at 20° C	6,000,000
4	Water added at 30° C	9,300,000
5	Water added at 40° C	6,700,000
6	Soil thawed in air at 1° C	5,000,000
7	Soil thawed in air at 10° C	6,100,000
8	Soil thawed in air at 20° C	6,300,000
9	Soil thawed in air at 30° C	6,900,000
10	Soil thawed in air at 40° C	5,800,000

SOILS FROZEN IN THE LABORATORY

Samples of soil that had been kept in a moist condition in the laboratory were used to test the effect of short periods of freezing and different rates of thaw. Counts were made of the normal soil containing 30 per cent of moisture, and the samples were then exposed to a temperature of −15° C. for twenty-four hours. In table 2 is shown the effect of short periods of freezing and different rates of thaw:

TABLE 2. EFFECT OF RATE OF THAW ON THE BACTERIA COUNT IN LABORATORY SOILS

Sample	Treatment	Bacteria per gram of dry soil
1	Normal	4,600,000
2	Frozen 2 hours at −16° C., thawed in room	6,600,000
3	Frozen 2 hours at −16° C., water added at 30° C.	9,800,000

There was an increase of about 50 per cent in the bacteria count when the soil was thawed by adding water at 30° C., over the count from the sample allowed to thaw in the air. This would seem to indicate a breaking up of the clusters of bacteria, due to the sudden change in temperature.

EFFECT OF ALTERNATE FREEZING AND THAWING ON BACTERIA COUNT

If there is a breaking up of the masses of bacteria when subjected to extreme temperatures, then alternate freezing and thawing should have some effect. In the test to determine this point the soil was placed in two containers 10 by 6 by 4 inches in size and divided into compartments by means of strips of paper. One of the containers was brought in each day and allowed to thaw at room temperature, counts were made of the bacteria per gram of soil in one of the compartments, and the container was then placed outside to freeze again. The outer container remained frozen during the experiment. The results are shown in table 3:

TABLE 3. EFFECT OF ALTERNATE FREEZING AND THAWING ON THE BACTERIA COUNT

Day	Treatment	Bacteria per gram of dry soil
First	Normal	4,500,000
Second	Frozen and thawed	7,000,000
Third	Frozen and thawed	8,100,000
Fourth	Frozen and thawed	10,200,000
Fifth	Frozen and thawed	11,200,000
Sixth	Frozen and thawed	11,100,000
Seventh	Frozen and thawed	11,900,000
Eighth	Continually frozen	8,900,000

The results shown in table 3 would seem to indicate that alternate freezing and thawing did have some effect, until the fifth day at least. After that there was little or no increase. There is one thing that must be taken into consideration in all these results, and that is the possibility that some of the bacteria may be killed by freezing and that the number as shown by the plate count may represent a greater breaking-up of the masses than the results would otherwise indicate. Inasmuch as the pots were only 4 inches deep, and the samples from which the counts were made

represented the bottom as well as the top of the soil, the increase could not have been due to the drawing-up of the organisms from the lower depths, as suggested by Harder.

EFFECT OF TIME, TEMPERATURE, AND RATE OF THAW ON BACTERIA COUNT

IN CLAY SOILS

The effect of the time of freezing and the rate of thaw on the number of bacteria in frozen soil, and on the bacteria in the dilutions from the soil, is shown in table 4. In the test to determine the latter, samples were taken from the flasks containing the last dilution — the one that was plated out — and were frozen for different lengths of time.

TABLE 4. EFFECT OF TIME, TEMPERATURE, AND RATE OF THAW ON THE BACTERIA COUNT IN CLAY SOILS

Sample	Treatment	Bacteria per gram of dry soil
1	Normal soil, water blank at 30° C	7,500,000
2	Normal soil, water blank at 0° C	6,800,000
3	Frozen 2 hours at −15° C., water added at 0° C.	5,600,000
4	Frozen 2 hours at −15° C., water added at 15° C.	7,100,000
5	Frozen 2 hours at −15° C., water added at 25° C.	8,200,000
6	Frozen 2 hours at −15° C., water added at 40° C.	5,800,000
7	Dilution of sample 1, frozen 1 hour	6,400,000
8	Dilution of sample 1, frozen 12 hours	4,300,000
9	Dilution of sample 1, stood 12 hours	5,700,000
10	Frozen in liquid air at −190° C. 1 minute	8,000,000
11	Frozen in liquid air at −190° C. 30 minutes	7,100,000
12	Frozen in liquid air at −190° C. 6 hours	3,400,000

The temperature of the water used in making the dilution seemed to have a marked effect on the bacteria in the frozen soil and a slight effect on the bacteria in the unfrozen soil. These results seem to indicate that the present method of making plate counts should be standardized, and that the temperature of the water blanks used is one of the factors that must be controlled if the results are to be comparable.

When the soil was frozen in liquid air at a temperature of −190° C. for one minute, there was a noticeable increase in the bacteria count which could not be accounted for by actual growth and multiplication.

When the exposure to liquid air was continued for several hours there was a decrease in the number of bacteria.

The effect of freezing seemed to be less harmful on the bacteria in the soil than on those in the soil dilution in the water blanks. When the freezing was continued for 12 hours there was a marked decrease in number of bacteria. It would seem that the more concentrated soil solution acted as a protective agency, and when the solution was weakened the effect of low temperatures was more marked.

IN SANDY SOILS

The soil used by Harder in his work was a rich sandy loam, and as his results were so marked it was thought advisable to compare a sandy loam soil with the Dunkirk clay soil. The results obtained when a light sandy soil was used are shown in table 5:

TABLE 5. EFFECT OF TIME, TEMPERATURE, AND RATE OF THAW ON BACTERIA COUNT IN SANDY SOIL

Sample	Treatment	Bacteria per gram of dry soil
1	Normal soil, water blank at 24° C	6,400,000
2	Frozen in liquid air 5 minutes, thawed at 1° C	4,800,000
3	Frozen in liquid air 5 minutes, thawed at 10° C	5,400,000
4	Frozen in liquid air 5 minutes, thawed at 24° C	6,800,000
5	Frozen in liquid air 5 minutes, thawed at 30° C	5,600,000
6	Frozen in liquid air 5 minutes, thawed at 38° C	4,800,000
7	Frozen in liquid air 1 minute, thawed at 24° C	5,400,000
8	Frozen in ice and salt 1 minute, thawed at 24° C	7,200,000
9	Frozen in ice and salt 2 hours, thawed at 24° C	14,000,000
10	Frozen in liquid air 2 hours, thawed at 24° C	11,600,000

There was the same increase in the bacteria count due to the rate of thaw as noted in the earlier work, and a drop in the bacteria count when the temperature of the water blanks was raised to 30° C. and above. When the soil was frozen in ice and salt for one minute, there was an increase of nearly one million bacteria per gram of soil over the count for the normal soil. When the soil was frozen for two hours in ice and salt, the count increased to 14,000,000, showing an increase of 120 per cent over the count for the normal soil. When the soil was frozen in liquid air for two hours there was also a marked increase. It is evident that this

increase could not have been due to growth and reproduction of the bacteria in the unfrozen soil solution, as suggested by Brown, but that it must have been due to the breaking up of the clumps of bacteria.

The results from the liquid-air treatment would indicate that there is a breaking up of the clusters of bacteria sufficient to show a marked increase above the number in normal soil. When it is considered that probably many of the bacteria were killed by the low temperature, it seems evident that the breaking-up process must be even greater than the plate counts indicate.

AMMONIFICATION AND NITRIFICATION IN FROZEN SOILS

In order to test the bacterial activities in frozen soils more carefully, the ammonifying and nitrifying powers of frozen soils were studied. Peptone and casein were added to the soils at the rate of $\frac{1}{2}$ gram to 100 grams of soil. The determinations of ammonia were made at the beginning of the experiment and at the end of five days. One-half of the samples were placed in the incubator at 22° C., and the other half were kept frozen during the experiment. The determinations of nitrates were made at the beginning of the experiment and at the end of four weeks. The samples were treated the same as in the ammonification experiment. The results are shown in table 6:

TABLE 6. AMMONIFICATION AND NITRIFICATION IN FROZEN AND IN UNFROZEN SOILS

Treatment	Parts per million of dry soil			
	Ammonia nitrogen		Nitrate nitrogen	
	At beginning of experiment	At the end of 5 days	At beginning of experiment	At the end of 4 weeks
Soil and peptone, frozen	65.4	68.7	112	118
Soil and peptone, incubated	65.4	382.9	112	253
Soil and casein, frozen	56.1	55.3	112	116
Soil and casein, incubated	56.1	336.9	112	237

These results show that there is little or no change going on in the soil solution when it is in a frozen state. This indicates that no protoplasmic activity, such as growth or reproduction, is taking place.

EFFECT OF LOW TEMPERATURE ON BACILLUS RADICICOLA

Since little or no work has been done in studying the effect of low temperature on pure cultures of the soil bacteria, it was deemed advisable to use the non-spore-bearing organism *Bacillus radicicola*, because of its economic importance. Since this is the organism used for inoculating the legume plants, it was thought that if low temperature does have a marked effect on its development, this fact might throw some light on the soil-inoculation question.

The method employed was to grow the bacteria in pure cultures in nutrient solutions, sand, and soil, and then subject them to different degrees of temperature for varying lengths of time. The nutrient solution used was the one recommended by Wilson (1917) in his studies of *Bacillus radicicola*. The saccharose in the original solution was replaced by mannite, using 1 gram per liter. The larger amount of sugar tended to increase the viscosity of the growth, which rendered it less favorable for quantitative work. The soil used was of the Dunkirk series. Counts were made by the agar-plate method. The medium used was the same as the nutrient solution mentioned above, with the addition of 1.5 per cent agar. The 10 grams of soil — or, in the case of the nutrient solution, 1 cubic centimeter — was added to water blanks until the desired dilution was obtained. Five plates were poured from each dilution, and three dilutions were used in all cases for pouring the plates. Separate counts were made in all cases and the averages of the five plates were taken for the final counts. The results in table 7 represent the findings on 1350 plates.

All freezing was done in thin-walled glass tubes. In the solution tests the bacteria were grown in the test tubes in which they were later frozen. Five-hundred-gram portions of the sterile soil and sand were inoculated with the bacteria and maintained for one week at 25° C. Tests were made of these samples by weighing out one-gram portions into sterile tubes and subjecting them to the low temperatures. The samples were then added to 500-cubic-centimeter water blanks, in a frozen condition. An attempt was made to keep uniform all conditions that were not being studied. By lowering the tubes gradually into the liquid air it was possible to freeze them without breaking the glass.

In interpreting the results shown in table 7, the fact must be kept in mind that the present method of determining the number of bacteria is very

unsatisfactory, especially when working with frozen soils. The colonies on the plate may represent a single cell or a mass of cells, and, altho the number of colonies may be greater after freezing, the investigator is not at all sure that a great many of the organisms have not been killed and that the seeming increase is due to the breaking up of the clusters.

TABLE 7. Influence of Low Temperature on Bacillus radicicola in Solution, Sand, and Soil Cultures

Sample	Treatment	Bacteria per cc. of solution	Bacteria per gram	
			Sand	Soil
1	Normal soil	3,000,000	3,700,000	400,000,000
2	Frozen with ice and salt at −15° C. 3 minutes	1,400,000	5,200,000	470,000,000
3	Frozen with ice and salt at −15° C. 1 hour	1,000,000	3,200,000	500,000,000
4	Frozen with ice and salt at −15° C. 2½ hours	750,000	3,000,000	520,000,000
5	Frozen with ice and salt at −15° C. 6 hours	600,000	2,800,000	400,000,000
6	Frozen in liquid air at −190° C. instantaneously	1,000,000	2,700,000	470,000,000
7	Frozen in liquid air at −190° C. 30 minutes	750,000	2,200,000	380,000,000
8	Frozen in liquid air at −190° C. 1 hour	620,000	2,100,000	360,000,000
9	Frozen in liquid air at −190° C. 2½ hours	600,000	2,600,000	530,000,000
10	Frozen in liquid air at −190° C. 6 hours	450,000	2,100,000	400,000,000

In table 7 it is shown that there is a gradual decrease in the number of bacteria in the solution as the degree of cold and the time of freezing is continued. In the sand cultures there was a marked increase in the number of bacteria when frozen for a few minutes at −15° C. This would indicate a breaking up of the clusters of bacteria that may surround the sand particles. A slight protective action was present in the sand and soil cultures that was not noticed in the solution cultures. The length of time of freezing had very little effect when liquid air was used. In sand the total count was slightly below normal, and remained so during the test.

The results obtained with the soil cultures are interesting and give some idea of what may be expected in such work dealing with the bacterial

flora of the soil. The results show no difference between the total counts of the normal soil and those of the samples that had been exposed to the temperature of liquid air for six hours, or those frozen with ice and salt for six hours. The samples exposed to the temperatures of –15° and –190° C. both showed a marked increase over that of the normal soil, again indicating a breaking-up process. It would seem that the non-spore-bearing bacteria, such as *Bacillus radicicola*, are able to withstand the effect of low temperature of the soil. Careful work on the bacterial-activity problem would doubtless verify this supposition. All evidence points to the probability that the effect of freezing on the soil is physical, not bacteriological.

INFLUENCE OF CONCENTRATION OF THE MEDIUM ON THE DEATH OF BACTERIA AT LOW TEMPERATURES

The results obtained with *Bacillus radicicola* in solution and soil cultures would seem to indicate that the concentration of the solution surrounding the bacteria had something to do with the ability of the bacteria to withstand low temperatures. The work of Maximow (1914) showed that such a protective action was evident when plants were placed in solutions of high concentrations. This protective action noted in the soil may have been due to the concentration of the soil solution or to some other factor such as the influence of surface tension on the large and the small soil particles.

If the death of the bacterial cell when frozen is due to the withdrawal of water from the semi-permeable membrane, or outer layer of the cell, resulting in the precipitation of the proteids, then it should be possible to overcome this harmful effect of freezing by increasing the concentration of the cell sap. The greater the concentration of the cell sap within the cell, the greater would be the osmotic pressure, the greater the power of inhibition, and the greater the resistance of the cell to low temperatures.

There is a possibility that the surface tension may be so great on the small particles that it would prevent the freezing of the solution. But when one considers that a pressure of 2600 atmospheres is necessary to prevent starch grains from absorbing water, and a pressure of 13,000 atmospheres is necessary to prevent water from freezing at –20° C., one realizes that if the surface tension does play an important part in the soil solution the pressure must be very great.

INFLUENCE OF GLYCERIN

If the protective action is due to the greater concentration of the solution, the addition of sugar or similar substances should have the same effect. In order to test the influence of the concentration of the medium, a very weak nutrient solution was prepared as follows: Dibasic potassium phosphate 0.05 gram, magnesium sulfate 0.05 gram, sodium chloride 0.05 gram, calcium sulfate 0.05 gram, distilled water 1000 cubic centimeters. Glycerin was added at the following rates: 0.01, 0.05, 0.1, 0.5, 1, 5, 10, and 15 per cent.

Test tubes containing 10 cubic centimeters of the above nutrient solution with glycerin added in increasing amounts, were inoculated with a culture of *Bacillus radicicola* and incubated for five days at 25° C. At the end of that period, counts were made of the number of bacteria per cubic centimeter in each tube, by means of the agar plates. The tubes were then frozen for thirty minutes in ice and salt at a temperature of −15° C. At the end of the half hour the tubes were thawed by placing them in water at 15° C., and were plated as in the preceding experiments. Care was taken to have all conditions uniform, for the earlier findings indicate that a difference in the temperature of the water blanks or in the rate of thaw might make a difference in these results. All counts were made at the end of five days incubation. Nine plates were poured from each tube and the experiment was run in triplicate, so that each count represents the average of twenty-seven plates.

TABLE 8. Influence of Glycerin on the Death of Bacteria When Frozen at −15° C.

Sample	Glycerin (per cent)	Normal bacteria count	Bacteria count after being frozen for 15 minutes	Per cent of bacteria killed
1	None	5,600,000	236,000	96
2	0.01	12,300,000	984,000	92
3	0.05	13,600,000	1,768,000	87
4	0.1	17,000,000	10,000,000	41
5	0.5	21,000,000	11,550,000	45
6	1.0	23,000,000	23,100,000	0
7	5.0	24,300,000	28,200,000	0
8	10.0	520,000	546,000	0
9	15.0	No growth	No growth	....

The results obtained when glycerin was used in varying amounts are shown in table 8. A remarkable protective action was exerted by the glycerin when the concentration was 1 per cent and above. With decreasing amounts of glycerin down to 0.01 per cent, there was a rapid increase in the percentage of bacteria killed. When the concentration of glycerin was raised to 5 and 10 per cent, there was an actual increase in the number of bacteria, as is shown by the colonies on the agar plates. This seeming increase was perhaps due to the breaking up of the clumps of bacteria. It is possible that in the nutrient solution containing 1 per cent of glycerin a great many of the organisms were killed, and that the high counts were due to the breaking up of the masses of bacteria. There was little or no growth in the nutrient solutions containing 15 per cent of glycerin.

INFLUENCE OF DEXTROSE

The results from the higher concentrations of media using glycerin and dextrose verified the finding of Maximow in his work with red cabbage and *Tradescantia discolor*. So long as the temperature of the frozen medium was maintained above the eutectic point of the substance used, the protective action was noted. If the above findings hold true in regard to the bacterial cell, the concentration of the medium should have no effect when the temperature is lowered to a point at which the glycerin and the dextrose will crystallize out. To test this latter point, the bacteria in the solutions described above were subjected to a temperature of −190° C., using ice and salt.

The results obtained with the different concentrations of media when exposed to a temperature of −190° C. using liquid air, and to a temperature of −15° C. using ice and salt, are given in table 9. There was the same marked protective action due to the increased concentration of the medium when the solutions were frozen in ice and salt for two hours, as was shown by glycerin (table 8). When the bacteria were subjected to the temperature of liquid air for five minutes the concentration of the medium had little or no effect. These results would seem to substantiate the foregoing theory, that when the temperature is lowered below that of the eutectic point of the sugars added, the concentration of the medium has no effect.

In table 9 the percentage of bacteria killed is based on the number of colonies growing on the plates poured before and after treatment of the

samples. The normal is considered as 100 per cent and the decrease is given as per cent killed. It is interesting to note that the concentration of the medium had no effect when the temperature was lowered below the eutectic point of the sugar, but at temperatures about the eutectic point the sugar showed a marked protective action.

TABLE 9. INFLUENCE OF DEXTROSE ON THE RESISTANCE OF BACTERIA TO LOW TEMPERATURES

Sample	Dextrose (per cent)	Normal bacteria count	Bacteria count when frozen in liquid air for 5 minutes	Per cent of bacteria killed	Bacteria count when frozen in ice and salt for 2 hours	Per cent of bacteria killed
1	None	No growth	....	......	....	......
2	0.01	880,000	570,000	35	17,600	98
3	0.05	1,960,000	1,240,000	37	98,000	95
4	0.1	3,600,000	2,400,000	33	398,000	89
5	0.5	4,700,000	2,490,000	47	1,220,000	74
6	1.0	16,400,000	9,480,000	42	6,890,000	58
7	5.0	24,100,000	16,390,000	32	15,660,000	35
8	10.0	11,300,000	8,140,000	28	10,850,000	4
9	15.0	8,200,000	4,670,000	43	8,000,000	2

GENERAL DISCUSSION

It is evident from the data given that the so-called increase in the number of bacteria in frozen soils is due, not to an actual multiplication and growth of the bacteria in the soil solution as suggested by Conn, but rather to a breaking up of the clumps of bacteria which results in an increased number of colonies on the agar plates. This view is substantiated by the fact that the same increase and decrease in counts may be obtained in the laboratory by freezing the soil for a few minutes and then thawing it out by means of water blanks at different temperatures.

The fact that the same marked increase may take place in soils when frozen in liquid air at a temperature of −190° C. for a few hours, invalidates Brown's theory that the increased growth takes place in the uncongealed hygroscopic water of the soil, for at this low temperature the amount of water remaining uncongealed could hardly be considered sufficient for the favorable growth of bacteria.

It is interesting to note that Conn's counts for the frozen soil were higher than those for the unfrozen soil, whereas the counts of Brown and Smith for the frozen soil were in all cases except one far below those for the unfrozen soil, and in the sample taken on March 1, in which the count was above normal, the moisture content had been increased from 15.76 to 26.57 per cent. Regardless of the fact that three samples out of the four taken showed a lower bacteria count than the normal soil, Brown and Smith concluded that their results substantiated the conclusion of Conn that bacteria do reproduce in increasing numbers in frozen soil.

It is interesting to note the very close correlation that can be drawn between the increase in the number of bacteria in frozen soils and the increase in the individual over the group counts, as shown by Conn in recent publications (1917 and 1918). In both cases the increase was between 25 and 50 per cent, the individual count showing the greater gains. The gains obtained by the author with the frozen samples are in very close keeping with the preceding.

The moisture content and the rate of thaw are the important factors that determine to a large extent the breaking-up process. This point is well brought out in the work of Harder. When the frozen soil was thawed rapidly by rain there were a large number of organisms occurring in the thawed soil, but when the thaw was gradual the number dropped back to about normal. The only high count obtained by Brown and Smith can be explained in somewhat the same manner. Their sample taken on February 11 showed a moisture content of 15.7 per cent and a bacteria count of 4,744,000 colonies; whereas their sample taken on March 1 showed a moisture content of 26.5 per cent and a bacteria count of 16,870,000. Between these two dates the moisture content rose 68 per cent, which would indicate that there had been a thaw followed by a freeze, resulting in a breaking up of the masses of bacteria.

That frozen soil is not as favorable a medium as unfrozen soil for the growth of bacteria is shown by the results obtained by Harder when soils were treated with dextrose. His results show a retardation in growth caused by low temperature, which even a much higher moisture content was not sufficient to counteract. They substantiate the theory that the increased count in frozen soils is due to a breaking up of the clumps of bacteria, for such an increase should be more marked in soils having a high moisture content and this condition was found to be true

in almost all cases. When the soil was thawed rapidly by rain, the count in the thawed soil was very much higher than when the thaw was gradual, indicating a breaking-up process due to the rapid thaw. When the conditions for an actual increase and growth were brought about by the addition of dextrose to the soil, the unfrozen sample showed a much greater increase in bacteria content than did the frozen sample. All this would seem to prove that frozen soil is not as favorable a medium as unfrozen soil for the growth of bacteria. That the increase is not due to mechanical transportation by moisture coming up from below during heavy frosts was shown by Conn in his work with potted soils, and also in the results herein reported, in which the same marked increase was obtained when small amounts of the soil were frozen in test tubes and an entire portion was used in making the dilutions.

The conclusions of Brown and Smith in regard to bacterial activities in frozen soils have not sufficient evidence to give them weight. It is interesting to note how their idea of a summer and a winter flora has been made to fit in with their results. Altho they concluded that the ammonifying power of the frozen soil is increased, the smallest amount of ammonia was produced from the sample taken during the coldest period of the tests. When it is considered that Brown and Smith used a soil infusion representing 5 grams of the frozen soil to inoculate 100 grams of air-dry soil, the results are not surprising. It would seem that the experiment under such conditions could better be called a study of the effect of storing air-dry soil on the bacterial flora therein, inasmuch as the number of bacteria present in the air-dry soil was several times that in the 5 grams of frozen soil. Duplicate tests might perhaps have eliminated the marked variations obtained by Brown and Smith. The tests that should have shown the difference, if there really was one, were those on nitrification, for the condition surrounding those tests are more easily controlled, and the measured product, nitrates, is not so easily lost as are some of the other products. The nitrification results of Brown and Smith indicated that if there was a difference their method was not sufficiently accurate to show it. It would seem that a similar conclusion may be applied to all their results.

Brown and Smith concluded from their nitrification results that the nitrifying power of the soil was rather weak. This is contrary to the findings of Lyon and Bizzell, who noted a beneficial effect due to freezing.

If there was active growth and reproduction of the ammonifying and other types of organisms in the soil, one would expect a protoplasmic activity that would be indicated quantitatively or qualitatively by the formation of ammonia and similar products. As no change was noticeable in the frozen soil, even when large amounts of nitrogenous materials were added, it would seem as if bacterial activities had ceased.

If the bacterial flora of the soil can withstand the low temperature of liquid air for several hours, it seems probable that the mild temperatures to which our soils are subjected during the winter would have little or no effect in changing the bacterial flora therein, and it will require more careful work than has yet been done on the bacterial activities in frozen soils to prove that such a change does take place.

The results obtained by investigators in the field of soil colloids seem to indicate a physical change in the soil due to freezing. It is probably this physical change in the soil and its colloids that influences the bacterial activities, rather than a change in the bacterial flora of the soil.

There is a possibility that pressure may play some part in cell division, for the soil is subjected to considerable pressure during the formation of ice from the soil solution. Kny (1896) noted that pressure actually induced cell division in the pith of Impatiens, and that very pronounced pressure will cause the periclinal divisions of the cambium to cease and anticlinal ones to appear. In many cases he found that pressure induced he formation of cell walls at right angles to its line of action. The close correlation between the high moisture content and the large number of bacteria occurring in the frozen soil seems to favor this theory, for the greater the moisture content, the greater would be the pressure. The fact that small quantities of soil placed loosely in test tubes and frozen showed the same increase, would, however, seem to indicate that the increase was not due to pressure.

The wide variations found by many careful investigators in their studies of the influence of low temperatures on bacteria, may be accounted for by the difference in the concentration of the media in which the bacteria were grown. The fact that 98 per cent of the organisms growing in a very rich nutrient solution survived the low temperature, would seem to support the theory that the higher the concentration of the medium surrounding the cell, the higher will be the concentration of the

cell sap within the cell, which in turn enables the cell to resist freezing at temperatures sufficiently low to freeze the cells containing a weaker solution.

SUMMARY

The increase in the bacteria counts of frozen soils, as determined by the agar-plate method, is due to the breaking up of the clumps of bacteria, not to growth and multiplication.

There seems to be no change in the bacterial flora of the soil due to freezing. The bacterial activities are influenced only in so far as the physical properties of the soil are affected.

The concentration of the medium, the length of time of the exposure, and the degree of cold, are the three important factors that determine the power of resistance of the bacteria to low temperature.

The protective action due to the concentration of the medium seems to be effective only in cases in which the eutectic point of the substances in solution is below the temperature of the exposure. When the bacteria were exposed to the temperature of liquid air the concentration of the medium had less effect.

The death of the bacterial cell when exposed to low temperature seems to be due to the withdrawal of water from the semi-permeable membrane, or outer layer of the cell.

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THE CARBON DIOXIDE OF THE SOIL AIR

H. W. TURPIN

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H. W. Turpin

Carbonic acid has long been recognized as an important soil solvent. On this point, at least, authorities are well agreed, but from the data available it is not yet clear what factors are most important in controlling the production of carbon dioxide in the soil. It is generally conceded, however, that a large proportion of the carbon dioxide found is due to soil microorganisms. The significance of plant roots in this connection has been recognized by some investigators, while others appear to be not quite decided as to how important plant-root excretions are.

HISTORICAL REVIEW

IMPORTANCE OF THE CARBON DIOXIDE IN THE SOIL

That carbon dioxide in solution is an important soil solvent has been shown by Stoklasa and Ernest (1909).[1] These workers point out that when ground gneiss and basalt are mixed with nutrient solutions, the amount of phosphorus and potassium absorbed by the plants grown is directly proportional to the carbon dioxide produced per gram of dry matter of the roots.

Aberson (1910) concluded, as a result of studies with young plants, that, while the excretions from plant roots may not be sufficiently concentrated (in carbon dioxide) to have a marked effect in dissolving insoluble materials, still the mucilaginous covering of the root hairs, containing a saturated solution of carbon dioxide, is entirely sufficient to bring into solution the insoluble soil constituents with which it comes in contact, especially the phosphates.

The limited usefulness, as a solvent, of the carbon dioxide secreted by plant roots is pointed out by Pfeiffer and Blanck (1912), who show that in soils treated with phosphates the carbon dioxide given off by plant roots is not a sufficient solvent to account for all the mineral nutrients obtained by the plant from the soil.

[1] Data in parenthesis refer to *Bibliography*, page 349.

Besides its importance as a direct solvent in the soil, carbon dioxide has considerable significance as an indicator of certain soil activities. Hutchinson (1912) observed a relationship between the biological activities and the amount of carbon dioxide in the soil. Russell (1915, a and b) noticed a close parallelism between the carbon-dioxide and the nitrate production in the soil, there being more of these constituents in spring and fall than in midsummer and winter. It was pointed out later by Russell and Appleyard (1915) that the curves for the bacterial numbers, the nitrate production, and the carbon-dioxide content in the soil thruout the season, show marked similarity, indicating that the carbon dioxide may serve to some extent as an indicator of other soil activities. Neller (1918), however, could find in his experiments no correlation between the ammonia production and the carbon dioxide formed, except in cases in which he used pure cultures of bacteria. The lack of correlation he attributed to the predominating influence of fungi in the soil.

In addition to its importance as a direct solvent in the soil and as an indicator of certain soil activities, carbonic acid may possibly be significant as an inhibitor of the activity of soil organisms and perhaps even of plant growth. Large quantities of carbon dioxide in the air have been found by numerous investigators to be detrimental to the growth of the higher plants. E. Wollny (1897) observed an increased production of carbon dioxide with an increase in the organic matter in the soil, but the increase to the unit of organic matter was less with the larger application. This Wollny attributed to the inhibiting effect of carbon dioxide on the bacterial activities. The work of Plummer (1916), however, showed that exceedingly large amounts of carbon dioxide do not interfere with the activities of the ammonifying and nitrifying organisms, provided, in the latter case, that the oxygen supply is not reduced below a certain minimum. The same investigator showed that the maximum carbon-dioxide production in the soil corresponds with the point of maximum nitrification. In studies on the carbon dioxide produced in lysimeter tanks, Bizzell and Lyon (1918) noted a marked decrease in the production of this gas after the blooming period of an oat crop on Dunkirk clay loam. This decrease, they say, "was apparently due to the depressing effect of the crop on production by bacterial action." Such a decrease was not found to take place on a Volusia silt loam.

FACTORS AFFECTING THE AMOUNT OF CARBON DIOXIDE IN THE SOIL AIR

Soil organisms

Most investigators consider that soil organisms play a large part in the production of carbon dioxide in the soil. Pettenkofer (1858, 1871, 1873, 1875) concluded, as a result of his investigations, that most of the carbon dioxide in the soil is due to living organisms.

Later, E. Wollny (1880b) found that there is only a small production of carbon dioxide in an atmosphere of hydrogen gas, while chloroform almost completely stops the power of the soil to form carbon dioxide. He concluded that carbon dioxide is produced largely by bacteria.

Further confirmation of this is to be found in the studies of Dehérain and Demoussy (1896), which showed that sterile soil at a temperature of 22° C. produces only insignificant amounts of carbon dioxide. Stoklasa and Ernest (1905), after working with beets, clover, oats, and other plants, noted that a bare soil produced, in one hundred and fifty days, more than twice the carbon dioxide produced by a crop of wheat on the same area in sixty days. They observed also a correlation between the numbers of bacteria and the carbon dioxide produced at different depths in the soil. Hutchinson (1912) concluded that carbon-dioxide production is a reliable measure of bacterial activity.

Soil conditions

Where soil conditions are favorable to the action of bacteria, the carbon-dioxide content is usually high. For example, Stoklasa (1911) obtained the greatest production of this gas in a soil that was well aerated, slightly alkaline, and well supplied with readily available plant nutrients. This was found by E. Wollny (1897), Russell and Appleyard (1915), and others, to be especially true in the case of soils having readily available organic matter. Very small amounts of carbon dioxide were found in the swamp rice lands of India by Harrison and Aiyer (1913), showing that unfavorable soil conditions are associated with a low content of carbon dioxide.

Seasonal conditions

Russell and Appleyard (1915, 1917) emphasized the importance of seasonal conditions on the carbon-dioxide content of the soil. In their investigations they observed that a rise of temperature is accompanied

by an increase in carbon dioxide. The same fact had been previously noted by Möller (quoted by E. Wollny, 1880a), by Dehérain and Demoussy (1896), by Stoklasa and Ernest (1905), and by Leather (1915), and was later mentioned by Potter and Snyder (1916).

Carbon-dioxide production was found by the Rothamsted investigators (Russell and Appleyard, 1917) to be correlated with moisture and rainfall. Previously E. Wollny (1880a) had observed that increasing amounts of water up to 9 per cent, in a quartz sand mixed with peat, resulted in an increase in the carbon dioxide. Dehérain and Demoussy (1896) found that there was an optimum water content for carbon-dioxide production in a garden soil. Van Suchtelen (1910) found the greatest amount of carbon dioxide when the soil with which he worked was 75 per cent saturated with water.

The relationship observed by Russell and Appleyard (1917) between the rainfall of the preceding week and the carbon-dioxide content of the soil, was believed by them to be due largely to the oxygen dissolved in the rain water. That this may be true is shown by the earlier work of E. Wollny (1897), and also by that of Fodor (1875), who showed that there is a relationship between the carbon-dioxide content and the oxygen of the soil, indicating that the carbon dioxide is probably produced by oxidation processes.

The crop

The evidence available thus seems to point to bacteria as the chief source of soil carbon-dioxide. There are some data, however, which show that plants may play a considerable part in the production of this gas in the soil.

Stoklasa and Ernest (1909) and Aberson (1910) noted that the roots of plants excrete large amounts of carbon dioxide. That the gas so formed is not insignificant is proved by the fact that field studies conducted at Rothamsted by Russell and Appleyard (1917) showed a considerably higher content of carbon dioxide in cropped soil than appeared in the bare soil, this being especially marked in May, at the time of the most active growth of the plant, and at the time of ripening. The same condition was observed by Bizzell and Lyon (1918) in the case of an oat crop on Dunkirk clay loam, where the greatest production of carbon dioxide took place at about the time of blooming. Potter and Snyder (1916) observed

similar results with timothy, but they were unable to decide whether or not this increase of carbon dioxide was due to the plant-root excretions or to the decay of root particles that had died during the growth of the crop. The work of Stoklasa and Ernest (1905) showed that the younger the plant is, the greater is the amount of carbon dioxide formed. Kossowitch (1904) noted that mustard grown in quartz sand and nutrient solutions produced an increased amount of carbon dioxide up to the time of blooming. This was observed also by Barakov (1910) in the case of plants growing in lysimeters.

That different kinds of plants produce different amounts of carbon dioxide has been shown by Lau (1906), who found that potatoes and legumes give off more carbon dioxide than do other crops. Red clover, beets (*Beta vulgaris*), and oats were found by Stoklasa and Ernest (1905) to produce more carbon dioxide than other plants, and in the order named. Russell and Appleyard (1915), however, could find no difference in the carbon-dioxide content of soils on which different species of plants were growing.

Chemical factors

From the brief survey given, it would seem correct to say that most of the carbon dioxide found in the soil is the result of biological activity. There is some evidence, however, showing that chemical action may play a small part. E. Wollny (1880 b) noted a very slight production of carbon dioxide in soil treated with chloroform. The same investigator demonstrated later (E. Wollny, 1897) that organic matter in the absence of oxygen reduces manganese and iron oxides and forms carbon dioxide. Very little carbon-dioxide production in sterilized soil kept at a temperature of 22° C. was observed by Dehérain and Demoussy (1896). They found, however, a very considerable production of carbon dioxide in soil heated to 90° C. and above. An oxidizing enzyme in the excretions of the root hairs was considered by Molisch (1888) to be capable of producing carbon dioxide from organic substances. It is probable that carbon dioxide produced by chemical means forms an extremely small part of the total carbon dioxide found in the soil.

Summary

In this review of the literature of the subject, certain facts stand out. Authorities are agreed that bacteria play an important part, probably

the most important part of all the factors concerned, in the production of carbon dioxide in the soil. Climatic factors, such as temperature, rainfall, and air supply, have a marked effect on the carbon-dioxide content of the soil. Crops increase the amount of carbon dioxide in the soil, either by direct excretions from the roots or thru the decay of root particles from the growing crop. Finally, the nature of the soil itself causes marked differences in the production of carbon dioxide.

The results reported in this paper confirm some of the above conclusions, but they also show that the influence of the crop has been underemphasized.

EXPERIMENTAL WORK

In the author's first experiment, a study was made for two seasons (1917 and 1918) in the greenhouse, with soil cropped to oats and with uncropped soil. The object was to try to establish some definite relationship between the carbon dioxide in a cropped soil and that in an uncropped soil, where the crop itself introduced the only variable. Such a relationship having been established, it was decided to determine in the second experiment whether or not it would hold for a different crop. The third experiment was designed to analyze the factors concerned in the production of carbon dioxide, and, if possible, to assign to each its respective part.

EXPERIMENT 1

The cylinders illustrated in figure 44 were used in the first experiment. These cylinders, eight in number, were made of galvanized iron, coated inside with a layer of paint to insure their being air-tight at the joints and to prevent rusting. They were 3 feet high by 1 foot in diameter, and each had a cone-shaped bottom leading to the cocks on the outside as indicated in figure 45.

The cone-shaped bottom was filled with gravel, above which was placed a 12-inch layer of soil from the second foot of the field soil. Above this was placed a foot of surface soil. The soil used was Dunkirk clay loam. The moisture in the soil was maintained thruout the course of the experiment at 30 per cent on the oven-dry basis. The soil was covered with a half-inch layer of quartz sand in order to reduce the evaporation, the sand being added to the cropped soil immediately after seeding. The dry weight of the soil in each of the cans was 94.3 pounds.

FIG. 44. CANS USED IN FIRST EXPERIMENT

The four cans at the left contain an oat crop, which is shown at the period of its growth a month before the maximum amount of carbon dioxide was found in the air of the cropped soil

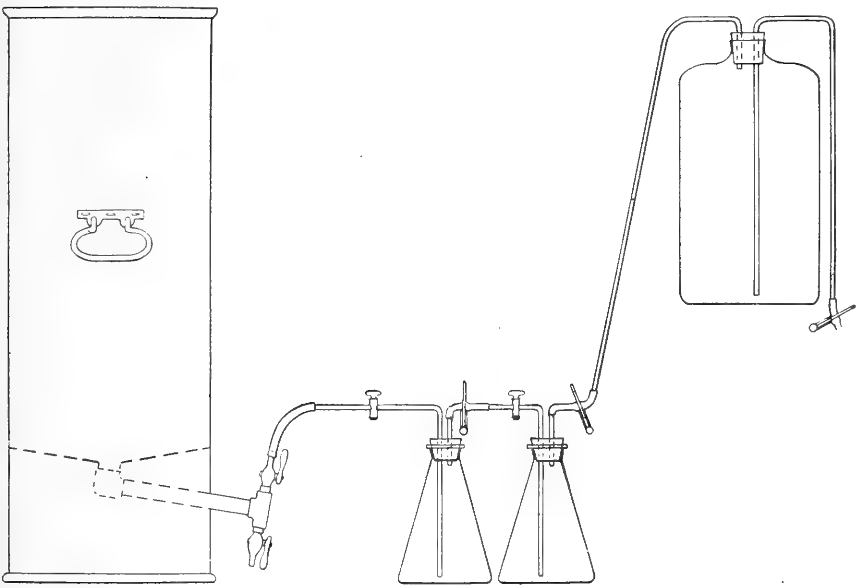

FIG. 45. ARRANGEMENT OF CYLINDER, SAMPLING FLASKS, AND ASPIRATOR

Before seeding, some preliminary studies were made in order to ascertain the best method of obtaining the sample of soil air for analysis. It seemed impracticable to use any method other than one that could be carried out rapidly, since it was planned to run the test for two seasons and to take the samples twice each week thruout the year. As a result of the preliminary studies, it was found that by aspirating four liters of air thru the soil cans in five minutes, and passing the air thru two graduated 500-cubic-centimeter Erlenmeyer flasks, samples could be obtained in the two flasks which checked with each other, indicating that the air originally present in the flasks had been replaced by a representative sample of the air in the soil. If more or less than four liters was aspirated thru the soil, the amounts of carbon dioxide in the two flasks did not check, indicating, in the first case, that the original air in the soil had been replaced by air from the atmosphere and that some of the latter was passing into the flasks, and in the second case that the original air in the flasks had not been completely replaced in the flask nearer the aspirator. The method of sampling is shown in figure 45. After the aspiration was completed, the cocks on the flasks were closed and the flasks were removed to the headhouse, where they were allowed to reach room temperature. The excess pressure in the flasks was relieved by opening one of the cocks for a moment. The temperature was noted at this point, as all calculations were reduced to per cent by volume of carbon dioxide at standard atmospheric conditions, that is, 760 millimeters pressure and 0° C.

Excess of standard barium hydroxide was next run into the flasks. The volume of the barium hydroxide added was noted, and was subtracted from the total volume of the flask. The cocks were then closed, and the flasks were allowed to stand, with occasional vigorous shaking, for about thirty minutes, after which the excess barium hydroxide was determined by titrating with standard oxalic acid whose equivalent in terms of carbon dioxide had been previously determined by titrating with standard potassium permanganate solution.

The method of aspirating air thru the soil has been criticized by Potter and Snyder (1916) in a paper describing experiments in which they determined the carbon dioxide evolved by drawing a current of air continuously over the soil surface. They maintain that the occasional drawing of air thru the soil will result in a temporary decrease in the content of carbon dioxide, which, however, will soon be restored by the

activities of the soil, and this accumulation of carbon dioxide will, by the mass action law, finally result in a retardation of further production of the gas. On the other hand, they maintain that by drawing a current of air continuously over the surface of the soil, conditions more nearly similar to those obtaining in the field will result. This may be true for experiments conducted in a quiet room; but in the greenhouse, where there is a circulation of air, there is ample opportunity for diffusion to take place from the soil, especially where, as in these experiments, one of the lower cocks of the soil can was always left open, so that a sample taken at any particular time should be truly representative of the carbon dioxide actually present under normal conditions.

It has been pointed out by Leather (1915) that usually only about 25 per cent of the carbon dioxide in the soil is in the gaseous state, the remainder being dissolved in water. It is reasonable to suppose that, once the soil water is saturated with this gas, any further production of carbon dioxide will tend to increase the content in the soil air. Considering these facts, then, it will be seen that the method used in these tests will not give, and was not intended to give, absolute amounts of carbon dioxide; but it nevertheless should yield reliable relative values.

On April 2, 1917, the soil, which is a heavy clay loam rich in silt and having a lime requirement of about 3000 pounds to the acre (Veitch), was brought up to 30 per cent moisture content on the oven-dry basis. Four of the cans were seeded to White Russian oats. A half-inch layer of quartz sand was then spread over the surface of the soil in the eight cans.

From April 12 to September 28 the samples were taken twice a week. From September 29 the sampling was done approximately once in two weeks until February 7, 1918, after which date the samples were again taken twice a week. The second crop of oats was planted on January 9. Some fifty seeds were usually sown, and the plants were thinned out in the course of two weeks to fifteen in each can. In the season of 1917, one plant became infected with smut, and on June 13 this plant was removed, together with one plant from each of the other cans. To maintain the moisture content of the cropped cans at 30 per cent (oven-dry basis) frequent waterings were necessary, especially at the time of most vigorous growth. At that period the cropped cans were irrigated once a day. The amount of water added was recorded in order to see whether or not there was any relationship between the transpiration and the carbon-

dioxide production in the cropped soil. Since only about a quarter of a pound of water was lost in a week from the uncropped soil, tap water was used in all cases, as the small loss by evaporation could not possibly introduce a disturbing element in the form of an accumulation of soluble salts in the soil.

Results

On each date of sampling, the samples were taken in duplicate from each of the eight cans. Thus eight samples were obtained from the cropped soil and eight from the bare soil. Since all of the four cropped cans were treated in identically the same manner, the data for the duplicate samples from the cropped cans were averaged. This was done also in the case of the bare soil.

It seemed fair to average the data obtained from the cans in each set because in all cases the differences were small. This is shown by the very small probable error. The data for the oat crops of 1917 and 1918 are given in tables 1 and 2 (appendix, pages 353 to 356), each figure for carbon dioxide in these two tables being the average of eight determinations. These summarized results are represented diagrammatically in figures 46 and 47.

Effect of crop

The content of carbon dioxide at the beginning of the experiment was 0.28 per cent by volume for both cropped and uncropped soil. From that time on, as may be seen from figures 46 and 47, the amount of carbon dioxide in the uncropped soil in no case reached that in the cropped soil — not even after the removal of the crop. The latter point may perhaps be explained by the fact that since the roots of the crop were not removed from the soil at harvesting, they somewhat increased the available supply of organic matter. The results reported here are directly opposite to those of Bizzell and Lyon (1918), who worked with the same Dunkirk clay loam under field conditions and found that subsequent to the removal of the oat crop a marked decrease in carbon dioxide below that in the uncropped soil took place. This was not found to be the case, however, with the Volusia silt loam used by these investigators.

A study of figure 46 shows that in the season of 1917 there was a marked increase in the carbon dioxide in the cropped soil from the beginning of May, a month after seeding, until the maximum, 2 per cent, was reached

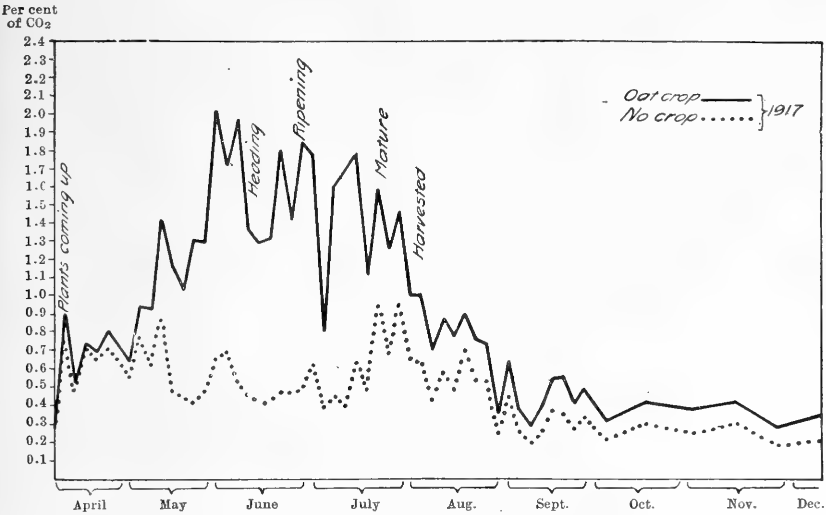

FIG. 46. CARBON DIOXIDE IN AIR FROM DUNKIRK CLAY LOAM CROPPED TO OATS AND FROM THE SAME SOIL LEFT BARE, 1917

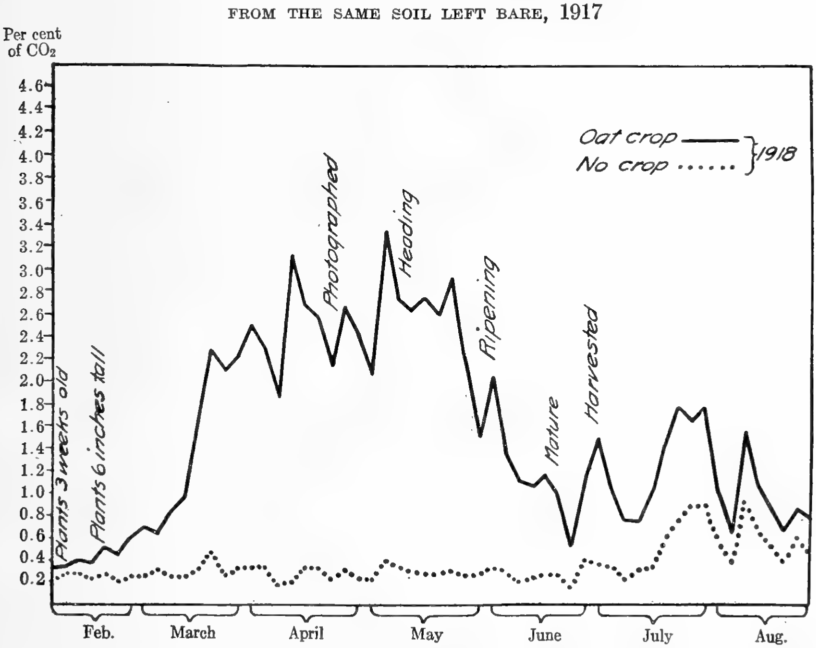

FIG. 47. CARBON DIOXIDE IN AIR FROM DUNKIRK CLAY LOAM CROPPED TO OATS AND FROM THE SAME SOIL LEFT BARE, 1918

in the first week of June, at the time when the plants were starting to head. Thereafter the general tendency of the curve for the cropped soil was toward a decrease, altho it was not until the middle of July, two weeks previous to harvesting, that this decrease was very marked. It was pointed out by Russell and Appleyard (1917) that in their experiments a large increase in carbon dioxide was observed in the cropped soil at the time of ripening; but, as can be seen from figures 46 and 47, in neither 1917 nor 1918 was any such increase noted in this work. If anything, the ripening was accompanied by a marked decrease in carbon dioxide, as is shown especially for the season of 1918 (fig. 47). Subsequent to the removal of the crop, the carbon dioxide in the cropped soil continued to decrease, but never to a point below or equal to that in the uncropped soil.

It is interesting to note that in 1917, fluctuations in the content of carbon dioxide in the uncropped soil were accompanied by similar variations in the cropped soil during the early part of the season and subsequent to harvesting. This was not true during the period of active growth of the plant, which would seem to indicate that at that time the life activity of the crop itself, rather than that of the soil organisms, is playing the dominant part in controlling the production of carbon dioxide.

What has been said for the season of 1917 holds for 1918 also. During the latter season, however, there was a much more marked increase in the carbon dioxide of the cropped soil. By the 11th of April, three months after seeding, more than 3 per cent of carbon dioxide was found, as compared with a little less than 0.2 per cent in the uncropped soil. This occurred four weeks previous to heading. Thereafter the content of carbon dioxide in the cropped soil increased to the maximum of 3.34 per cent, which occurred a week before heading and coincident with the time of rapid elongation of the culms. Following the maximum there was a steady decline. The decrease was especially marked during early June, when the upper glumes were beginning to turn yellow and the plants were starting to mature. In figure 44 (page 325) the plants are shown a month before the period of maximum carbon-dioxide production.

Since the maximum of 3.34 per cent of carbon dioxide found in the soil was about the same as that noted by Bizzell and Lyon (1918) in their studies with Dunkirk clay loam cropped to oats, it is evident that the decrease in the production of carbon dioxide in the cropped soil below

that in the uncropped soil after the removal of the crop, reported by these investigators, may not be due to interference with bacterial activities, since in the work reported in the present paper no such action on the soil organisms, as evidenced by a decrease in carbon-dioxide production, was observed. It may be possible that the decrease noted by Bizzell and Lyon was due to some other effect of the crop, such as, for example, the reduction of the soil moisture. It has been pointed out in the review of the literature of the subject that some investigators have noted a decrease in carbon dioxide where the moisture was reduced below a certain optimum amount. On referring to figure 46 it will be seen that early in July, 1917, the carbon dioxide in the cropped soil showed a marked decrease. This was due to the drying-out of the soil when, thru an oversight, it was not watered for two days.

It has been pointed out that the carbon dioxide in the cropped soil was somewhat higher (about 30 per cent) in 1918 than it was in 1917. The results for the two seasons are not strictly comparable, because in 1917 the crop was sown in April whereas in 1918 the seeding was made in January. Also, in 1917 the number of plants was reduced to fourteen in each pot, while in 1918 there were fifteen. However, the total dry weight of the mature crop from the four cans in 1917 was 494.5 grams, as against 416 grams in 1918.

Carbon-dioxide and water relationships

As has already been stated, a record was kept of the amount of water added to the cropped cans in order to maintain them at a moisture content of 30 per cent (oven-dry basis). The sand mulch on the soil, as has been pointed out also, was so effective that the loss in moisture on the cropped cans could be regarded as due entirely to transpiration.

The total amount of water lost on the cropped cans each week was determined in 1917 and 1918 for a period of ten weeks during which the crop was making the most active growth. These amounts, together with the average weekly content of carbon dioxide in the cropped and the uncropped soil, are indicated in tables 3 and 4 (appendix, pages 357 to 358), columns A, C, and E. The difference between the carbon dioxide in the cropped and that in the uncropped soil is given in column F of the same tables. The carbon dioxide produced to each pound of water used is shown in columns G and H. The figures in column G were obtained

by dividing the weekly carbon-dioxide percentage in the cropped soil after the carbon dioxide in the bare soil had been subtracted, by the weekly loss of water in pounds. The figures in column H, however, were obtained by dividing the weekly carbon-dioxide percentage in the cropped soil by the weekly loss of water without first subtracting the carbon dioxide in the bare soil from that in the cropped soil.

The relationship between the carbon dioxide produced in the cropped soil (from which has been subtracted the carbon dioxide in the bare soil), and the water transpired by the crop, is shown graphically in figures 48 and 49. There seems to be a relationship between the amount of water transpired and the carbon dioxide produced by plants, as is indicated

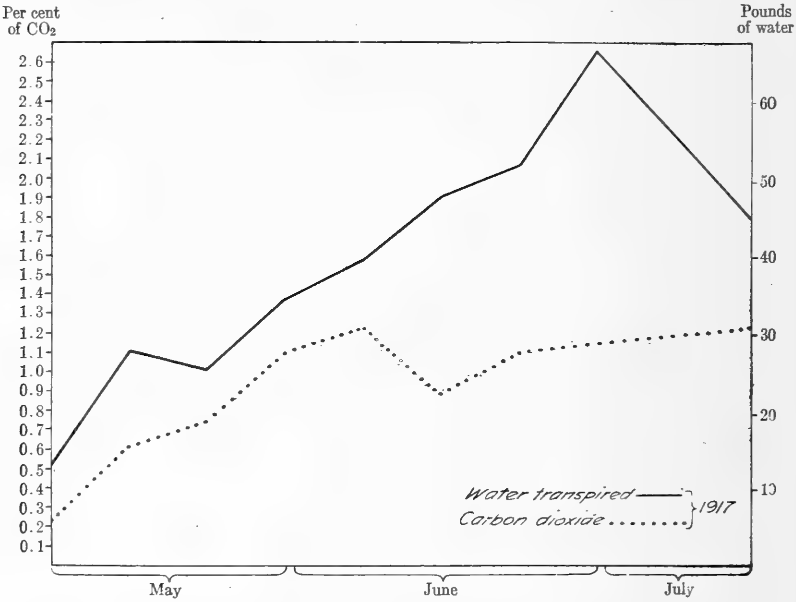

FIG. 48. RELATION BETWEEN WATER TRANSPIRED AND CARBON DIOXIDE PRODUCED BY AN OAT CROP FOR THE TEN WEEKS DURING WHICH ITS GROWTH WAS MOST VIGOROUS, 1917

by tables 3 and 4 and by figures 48 and 49. The illustrations show that the curves for the water transpired each week, and for the carbon dioxide obtained by subtracting the carbon dioxide in the bare soil from that in the cropped soil, follow each other closely. The data given in the

tables and plotted in the curves are for the period of ten weeks during which the plants were growing most actively. Before and after this period no relationship was found to exist between the amount of water transpired and the carbon dioxide produced by the plants.

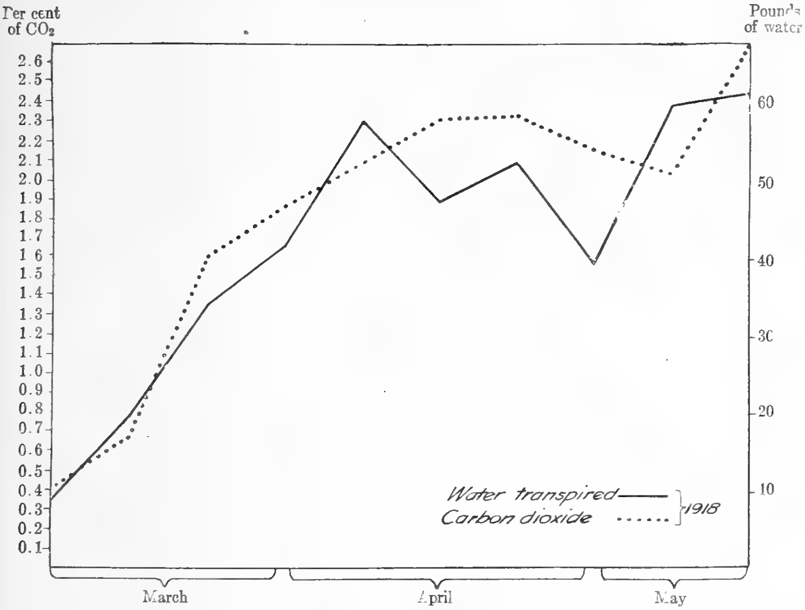

FIG. 49. RELATION BETWEEN WATER TRANSPIRED AND CARBON DIOXIDE PRODUCED BY AN OAT CROP FOR THE TEN WEEKS DURING WHICH ITS GROWTH WAS MOST VIGOROUS, 1918

It is seen in columns G and H of tables 3 and 4 that the percentage of carbon dioxide produced to each pound of water transpired, approaches a constant much more nearly when the carbon dioxide in the uncropped soil is subtracted from that in the cropped soil. The smaller coefficients of variability of 22.5 ± 3.74 as compared with 37.4 ± 5.65 in 1917, and 15.1 ± 2.32 as against 19.17 ± 3.12 in 1918, bring out this fact fairly clearly. If it is assumed that the amount of carbon dioxide produced and the amount of water transpired are indications of life activity, then the relationships found between the carbon dioxide in the soil, and the water transpired, would hold only when the carbon dioxide is produced

by the crop alone. When the carbon dioxide in the uncropped soil was subtracted from the carbon dioxide found in the cropped soil, and this figure was divided by the amount of water transpired, there resulted approximately a constant of 0.024 $\pm$ .0012 (column G) with a coefficient of variability of 22.5 $\pm$ 3.74 for 1917, and a constant of 0.043 $\pm$ .0014 with a coefficient of variability of 15.1 $\pm$ 2.32 for 1918. When the carbon dioxide in the uncropped soil, which may be attributed to bacterial activity, was not subtracted (column H), there resulted a constant of 0.042 $\pm$ .0031 with a coefficient of variability of 37.4 $\pm$ 5.65 for 1917, and a constant of 0.053 $\pm$ .0022 with a coefficient of variability of 19.17 $\pm$ 3.12 for 1918.

This shows that the constants in the latter cases are not nearly so dependable as those in the former, indicating that the carbon dioxide produced by the crop is probably the difference between the carbon dioxide in the cropped soil and that in the bare soil. That the values obtained are not perfect constants can hardly be wondered at when it is recalled that the carbon dioxide as determined was not absolute, but relative.

In this connection it may be pointed out that there seems to be some ground for concluding that there is a relationship between the water transpired by the plant and the carbon-dioxide content of the soil.

While it is not disputed that the mechanism by which the water is actually lost from the leaves of the plant is purely physical and not at all associated with vital plant activity, yet the process by which the water is brought into the leaves and into a condition to be transpired may well be considered as being associated with the life activities of the plant. Many investigators have maintained that there is a distinct relationship between the life activities of plants and the water transpired. For example, as early as 1849 Lawes (1850) considered that the comparative rate of transpiration of water to some extent indicated the relative activity of the processes of the plant. He drew these conclusions from studies with wheat, barley, beans, peas, and clover, in which he compared the amount of ash and dry matter obtained from the plants with the water given off by them. He found that the larger the amount of dry matter, the greater was the quantity of water transpired. These views are supported by the investigations of Sorauer (1878, 1880), but the work of Walter Wollny (1898) leads to an opposite conclusion. In 1905 Livingston (1905) worked with wheat seedlings and concluded that total transpiration is as good a criterion for comparing the relative growth of plants in

different media as is the weight of the plant itself. Hasselbring (1914), however, after growing plants under cheesecloth and in the open, stated that the mere passage of water thru the plant had no influence on the assimilatory activity of the plant, provided the water supply did not fall below a certain minimum required to maintain turgor of the cells. Stoklasa and Ernest (1909) determined the carbon dioxide given off by different plants grown in various nutrient solutions, and obtained the results presented in table 5 (appendix, page 358). These figures show that there is a definite relationship between the total dry weight of different crops and the carbon dioxide produced. The average of 0.037 milligram of carbon dioxide to each milligram of dry matter seems to be independent of the kind of plant used in the test.

From the short review given, it would seem that the evidence is in favor of the assumption that transpiration is related to life activity of plants as indicated by a relationship between the dry matter and the water transpired. The work of Stoklasa and Ernest (1909) would point to a correlation between the carbon dioxide produced and the dry matter in the plant.

Effect of temperature and atmospheric pressure

The relationship between the temperature and the atmospheric pressure at the time of sampling, and the carbon dioxide in the air of the uncropped soil, is shown graphically in figures 50 and 51 for the seasons of 1917 and 1918, respectively. The temperature at each time of sampling was found to be approximately representative of the temperature for the preceding twelve-hours period. The pressure also would probably represent the average of several hours preceding the sampling.

On the whole the figures bring out only a few striking facts. High temperatures were usually accompanied by a high percentage of carbon dioxide, while high atmospheric pressures were usually associated with a low carbon-dioxide content. High pressures along with high temperatures gave fairly high contents of carbon dioxide, indicating that temperature has a more marked effect than pressure. When the temperature and the pressure were medium there appeared to be no relationship with the carbon-dioxide content. Very low temperatures were always accompanied by a low content of carbon dioxide; but, while a very low pressure did not necessarily mean a high carbon-dioxide content, it was usually associated with such a condition.

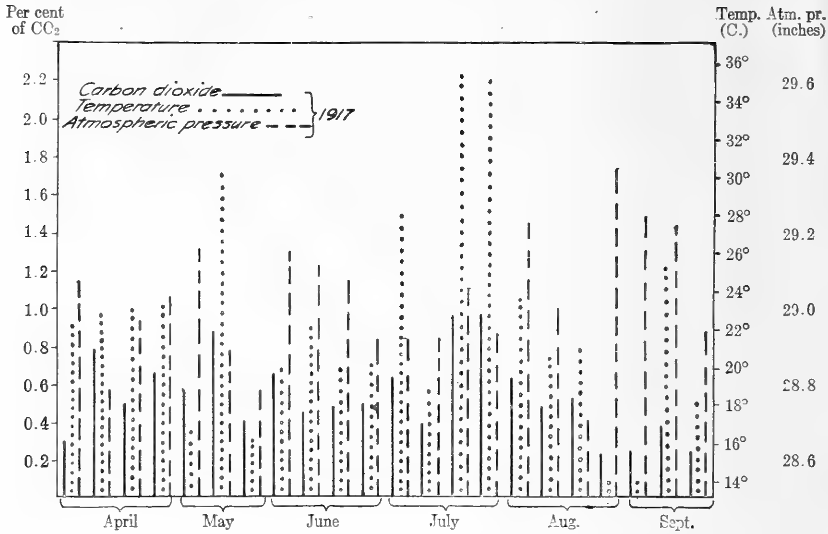

FIG. 50. RELATION BETWEEN THE TEMPERATURE OF THE SOIL AT THE TIME OF SAMPLING, THE ATMOSPHERIC PRESSURE, AND THE CARBON DIOXIDE IN THE AIR OF THE UNCROPPED SOIL, 1917

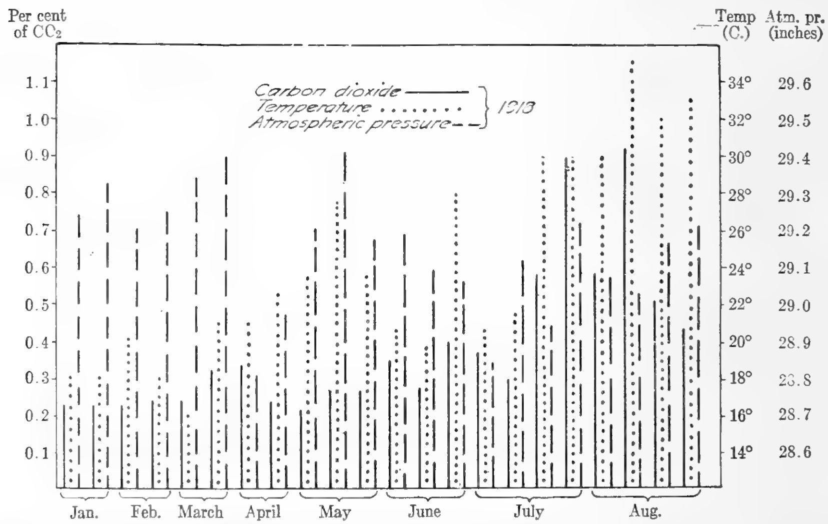

FIG. 51. RELATION BETWEEN THE TEMPERATURE OF THE SOIL AT THE TIME OF SAMPLING, THE ATMOSPHERIC PRESSURE, AND THE CARBON DIOXIDE IN THE AIR OF THE UNCROPPED SOIL, 1918

Summary of experiment 1

The results of the first experiment may be summarized as follows:

1. Soils cropped to oats always contained a greater amount of carbon dioxide than did the corresponding bare soils.

2. The crop had a residual effect, increasing the carbon-dioxide content above that in the uncropped soil.

3. The difference between the amount of carbon dioxide in the cropped soil and that in the uncropped soil at the period of most active crop growth, divided by the amount of water transpired by the crop, gave an apparent constant which varied with the season.

4. The fact just stated may indicate that the difference between the amount of carbon dioxide produced in the cropped soil and that in the uncropped soil represented the amount produced by the crop.

5. It is thus evident that the carbon dioxide from plants and from soil organisms accumulated independently.

6. Fluctuations in the amount of carbon dioxide in the uncropped soil were due largely to temperature and pressure variations. High pressures produced low contents of carbon dioxide, while high temperatures caused high production of carbon dioxide, and vice versa.

EXPERIMENT 2

The object of the second experiment was to determine the influence of some crop other than oats on the production of carbon dioxide. The crop used in this case was common millet (*Setaria italica*).

Immediately after the harvesting of the 1918 oat crop, millet was planted on the same soil and in the same cylinders as were used in experiment 1. For experiment 2 the surface layer of sand was entirely removed from the soil, which was then thoroly stirred to a depth of about three inches. The millet was seeded on four of the soils, of which two had previously been in oats and two had been bare. The object in using these two different sets was to try to produce some differences in the two crops of millet. It was thought that possibly the millet growing on the soil which had been previously cropped twice to oats, might not grow well, and in such a case a comparison could be made between a good and a poor crop of millet.

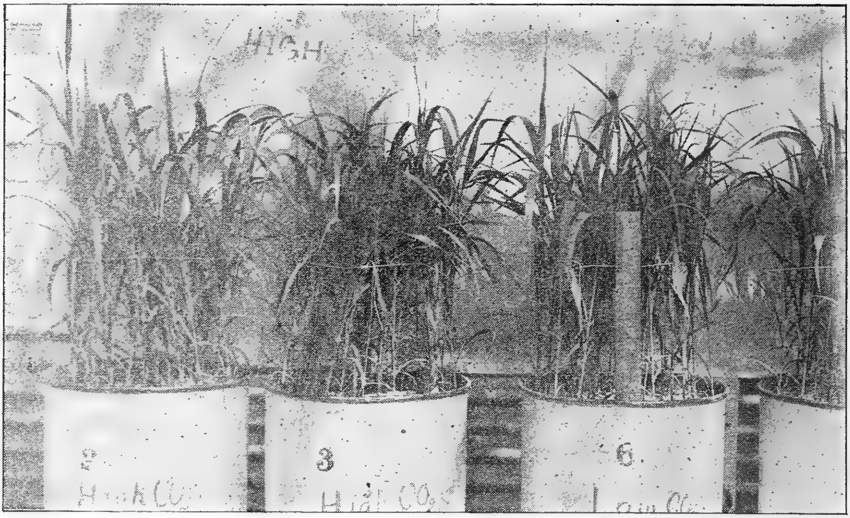

FIG. 52. MILLET CROPS SIX WEEKS AFTER SEEDING, ON THE TWO SOILS HAVING HIGH AND LOW INITIAL CONTENTS OF CARBON DIOXIDE, RESPECTIVELY

Close view, showing details

The crop was planted on July 1. Within three weeks after planting, the crop on each can had been thinned out until forty plants remained. The number of plants to a pot was reduced in the next week to thirty. At first the samples were taken twice a week, as in the case of experiment 1; but later — from the middle of August — when the crop was making very rapid growth, samples were taken every day. Toward the end of August the samples were taken every other day. As in experiment 1, the moisture in the soil was maintained at 30 per cent (oven-dry basis).

At the time when the experiment was discontinued, the plants were completely headed. In the case of series 1 (soil previously cropped to oats) the plants were beginning to show signs of maturing; in series 2 (soil previously bare), however, the grain was still between the milk stage and the dough stage.

The crops on series 1 and 2 were identical in all details until a few days after heading. This may be seen in figures 52 to 55. Thereafter the plants in series 2 maintained their dark green color, while those in

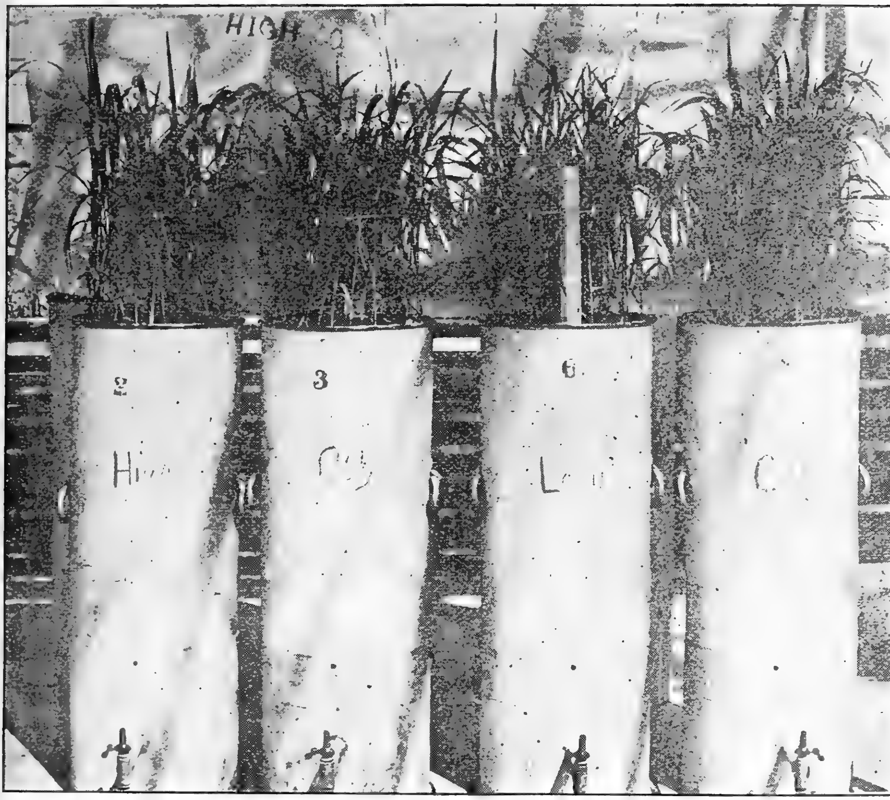

FIG. 53. MILLET CROPS SIX WEEKS AFTER SEEDING, ON THE TWO SOILS HAVING HIGH AND LOW INITIAL CONTENTS OF CARBON DIOXIDE, RESPECTIVELY

Same as figure 52, but showing cylinders

series 1 gradually became light green, until finally, when the experiment was stopped in September, the latter were beginning to mature while those in series 2 had not yet begun to show signs of ripening.

Results

The results of experiment 2 are summarized in table 6 (appendix, page 359), in which each figure represents the average of two duplicate samplings from each of two pots, an average of four samplings in all.

FIG. 54. MILLET CROPS SEVEN AND ONE-HALF WEEKS AFTER SEEDING, ON THE TWO SOILS HAVING HIGH AND LOW INITIAL CONTENTS OF CARBON DIOXIDE, RESPECTIVELY

Close view, showing details

These data are presented diagrammatically in figures 56, 57, and 58, the first two representing the data for series 1 and 2, respectively, and the third giving these two sets of curves on one sheet.

It will be noticed that the carbon dioxide in the cropped soils and that in the uncropped soils remained the same for the first four weeks after seeding. Thereafter the curves for the cropped soils separated fairly rapidly from those for the bare soils. In this respect there is no difference between the oats and the millet. It will be observed, however, that whereas the two oat crops attained their point of maximum carbon-dioxide production shortly before heading, the millet crops both gave the most carbon dioxide just ten days after heading. In order to bring out this point more clearly, curves showing the relationship between the amount of carbon dioxide in the oat soil (1917) and that in the millet soil (series 2) have been plotted together in figure 59, in such a manner that the carbon dioxide produced at the period of heading of each of the two crops is on the same ordinate, with the data for a few weeks

FIG. 55. MILLET CROPS SEVEN AND ONE-HALF WEEKS AFTER SEEDING, ON THE TWO SOILS HAVING HIGH AND LOW INITIAL CONTENTS OF CARBON DIOXIDE, RESPECTIVELY

Same as figure 54, but showing cylinders

before and a few weeks after the heading period plotted to the left and to the right of this point, respectively.

Since the experiment was discontinued before the millet crops matured, it is not possible to say whether or not the curve for the later period of

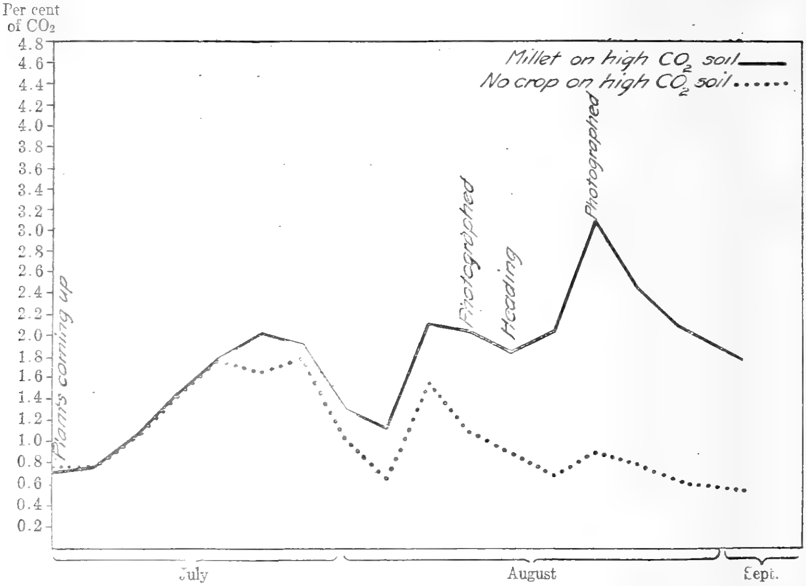

FIG. 56. CARBON DIOXIDE IN AIR FROM DUNKIRK CLAY LOAM PREVIOUSLY CROPPED TWICE TO OATS, CROPPED TO MILLET, AND FROM THE SAME SOIL LEFT BARE, 1918

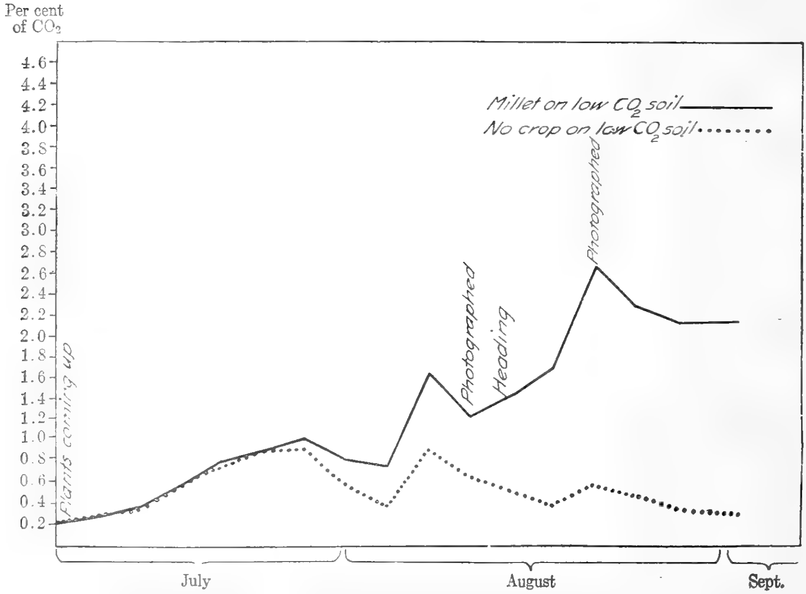

FIG. 57. CARBON DIOXIDE IN AIR FROM DUNKIRK CLAY LOAM NOT PREVIOUSLY CROPPED, CROPPED TO MILLET, AND FROM THE SAME SOIL LEFT BARE, 1918

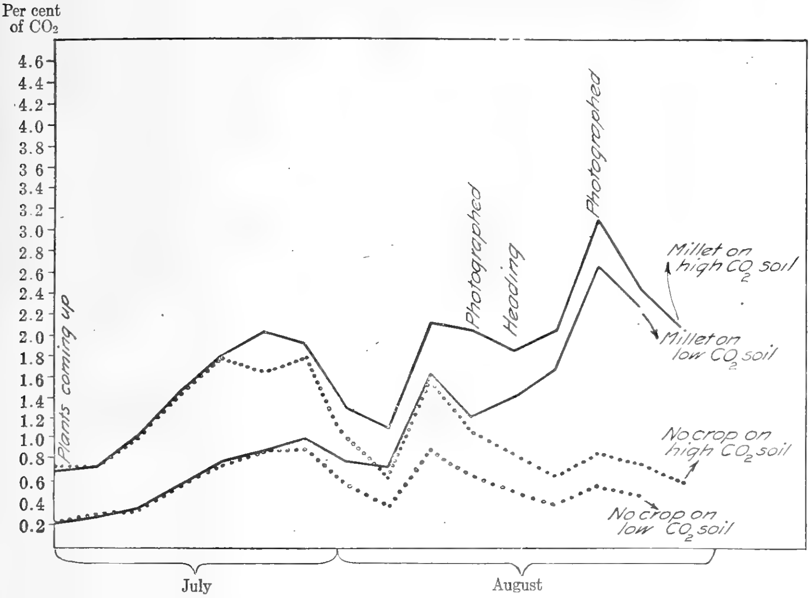

FIG. 58. RELATION BETWEEN THE AMOUNTS OF CARBON DIOXIDE IN AIR FROM CROPPED AND FROM UNCROPPED DUNKIRK CLAY LOAM HAVING HIGH AND LOW INITIAL CONTENTS OF CARBON DIOXIDE, RESPECTIVELY

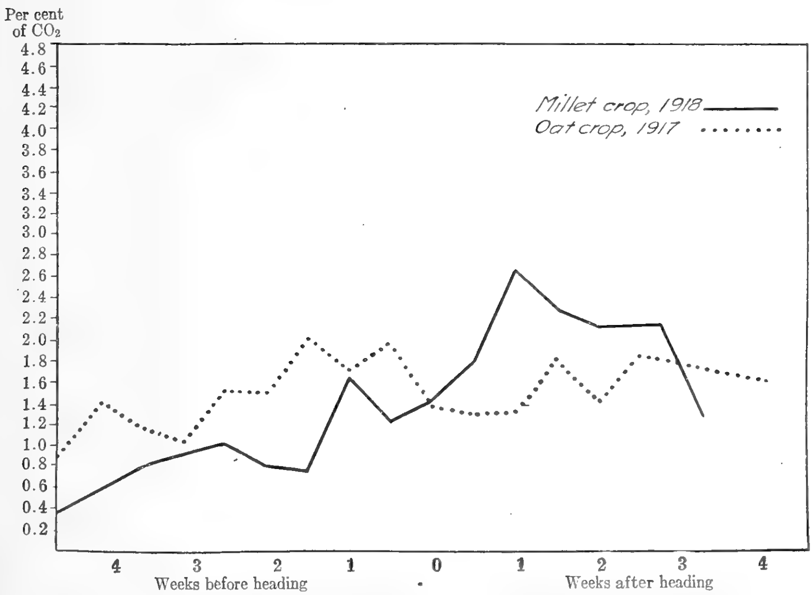

FIG. 59. RELATION BETWEEN THE AMOUNTS OF CARBON DIOXIDE IN AIR FROM DUNKIRK CLAY LOAM CROPPED TO OATS AND MILLET, RESPECTIVELY, BEFORE AND AFTER THE CROPS HEADED

growth of the millet would resemble in general that for the oat crops. The general tendency of the curve after August 25 was to fall as the plants advanced toward maturity, as in the case of the oat crops. It will be noticed from figure 59 that the actual amount of carbon dioxide produced on the soil cropped to millet was much the same as that produced on the oat soil. The maxima for the two oat crops of 1917 and 1918 were, respectively, 2.031 per cent and 3.343 per cent, while the corresponding figures for the millet crops in series 1 and 2 were 3.345 per cent and 2.715 per cent. It must be remembered, however, that there were but fifteen oat plants as compared with thirty millet plants; so that it may be concluded that an individual oat plant causes the production of about twice as much carbon dioxide as is produced by a millet plant.

Summary of experiment 2

From the results of the second experiment it may be concluded that a soil cropped to millet causes about the same fluctuations in carbon-dioxide production as are found in a soil growing an oat crop. In general, however, the oat crop gives the greatest production of carbon dioxide previous to heading, while the millet has its most marked effect a week or two after heading. It would seem also that an individual millet plant causes the production of approximately half as much carbon dioxide as an individual oat plant. From the close agreement between the two curves shown in figures 56, 57, and 58, for series 1 and 2, it may be assumed that in spite of slight differences in the previous treatment of the soil the excess carbon dioxide due to the crop was fairly similar where the crops growing showed no apparent differences in vigor. This is indicated also in figures 52 to 55, which show the two crops at an early and at a later stage of growth, the crop on the soil previously cropped twice to oats being designated as a high-carbon-dioxide crop and that on the soil that was previously bare being called a low-carbon-dioxide crop.

EXPERIMENT 3

As is pointed out in the review of literature, it is not clear whether or not the increased amount of carbon dioxide observed in a cropped soil is due to the excretion of carbon dioxide by plant roots (plant activity) or to the decay of root particles from the growing crop (bacterial activity). Data obtained in experiment 3 seem to throw a little light on this question. In this experiment, cans 1, 2, 3, and 4, which had previously grown two

crops of oats, had a considerably higher content of carbon dioxide, even after the removal of the crop and especially for about two months after harvest, than did cans 5, 6, 7, and 8, which remained uncropped for the two seasons.

After the oat crop from cans 1, 2, 3, and 4 was harvested, on July 1, 1918, cans 2 and 3, and the uncropped cans 6 and 8, were seeded to millet. Cans 1, 2, 3, and 4 are here designated as the high-carbon-dioxide series, while cans 5, 6, 7, and 8 are called the low-carbon-dioxide series. Thus, in the high-carbon-dioxide series, cans 1 and 4 were bare and cans 2 and 3 were cropped to millet; in the low-carbon-dioxide series, cans 5 and 7 were bare and cans 6 and 8 were cropped. All these cans were sampled in the usual way for carbon dioxide, and the data obtained are given in table 7 (appendix, page 360). The samples were taken twice a week at first, and later they were taken daily. The moisture in the soil was maintained at or near 30 per cent (oven-dry basis).

Within a month of seeding, the crop was thinned to thirty plants to a can; so that at the time when the effect of the plants on the carbon dioxide became noticeable (a month after seeding), the number of plants was the same for all cans.

Results

In table 7 it is shown that the differences between the percentages of carbon dioxide in the cropped soil and those in the uncropped soil in the high-carbon-dioxide series, were approximately the same as the corresponding differences in the low-carbon-dioxide series. In table 8 (appendix, page 361) it is seen that the majority of the differences in carbon-dioxide production by the crop in the two series (as determined by the difference between the amount of carbon dioxide produced by the cropped soil and that produced by the uncropped soil) was well within the limits of the experimental error. It seems, therefore, that the crops produced carbon dioxide quite independently, and that this production was not affected by the amount of carbon dioxide in the soil, at least not within the limits set by this experiment. How closely the difference between the curves for the cropped soils corresponded with those for the bare soils is shown in figure 58 (page 343).

The relationship between the temperature of the soil at the time of sampling, and the carbon dioxide in the bare soil and also that due to the crop on the low-carbon-dioxide series (determined by the difference as

explained above), is shown in table 9 (appendix, page 362) and in figure 60. It will be noticed that increases in temperature were more frequently accompanied by rises in carbon dioxide in the bare soil (indicating a relationship between bacterial activity and carbon-dioxide production), than by rises in the carbon dioxide produced by the crop. In the latter

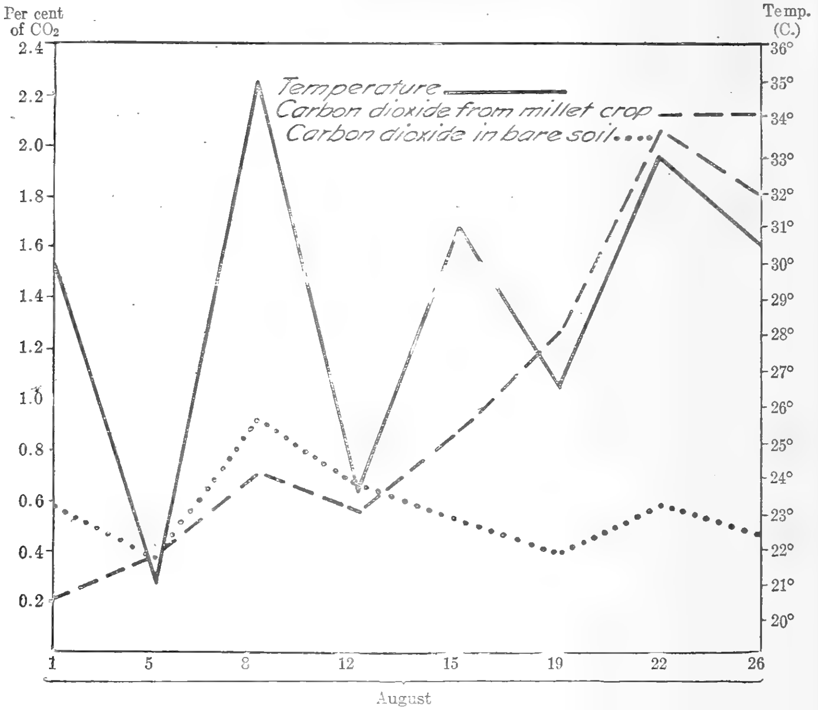

FIG. 60. RELATION BETWEEN THE CARBON DIOXIDE PRODUCED BY A MILLET CROP, THE CARBON DIOXIDE IN A BARE SOIL, AND THE TEMPERATURE OF THE SOIL AT THE TIME OF SAMPLING, 1918

case no such close relationship appeared, but the carbon dioxide increased gradually as the age of the plant advanced until the point of maximum carbon-dioxide production, after which there was a decline. This increase in carbon dioxide seems to have kept pace with the rate of growth of the plants. At the time when the plants ceased to grow actively (some time after heading), the carbon-dioxide production also fell off. If the excess

carbon dioxide in the cropped soil is due to the decomposition by bacteria of root particles thrown off from the growing crop, then one would expect to find that those factors which produce fluctuations in the carbon dioxide in the bare soil would produce corresponding, but more magnified, fluctuations in the cropped soil. But, as is pointed out above, a factor such as temperature did not produce corresponding changes in the two soils.

Again, if the decomposition of root particles from the growing crop gave rise to the increase of carbon dioxide in the cropped soil, it is reasonable to suppose that there would be a much larger increase in carbon dioxide at a time when the roots were beginning to die off rapidly, that is, toward the ripening period. Such, however, was not the case.

Summary of experiment 3

It is probable, therefore, that the larger part of the excess carbon dioxide produced in a cropped soil is due to respiratory activities of the plant roots, and that the amount resulting from the decay of root particles from the growing crop is small—altho after the crop has matured, any excess of carbon dioxide found is undoubtedly due to the decay of the mass of roots left in the soil. This excess, however, is very small when compared with the very large amounts of carbon dioxide found in the cropped soil at the time of heading, for example.

In support of the conclusion that the larger production of carbon dioxide in the cropped soil is due to respiratory activities of the plant roots, the data presented in experiment 1 show that there seems to be a correlation between the water requirements of the plant and the amount of carbon dioxide produced.

GENERAL SUMMARY

The results of the work reported in this paper with regard to the effect of crop and other factors on the production of carbon dioxide in a Dunkirk clay loam maintained at a constant moisture content of 30 per cent (oven-dry basis), may be summed up as follows:

1. An oat crop increased the production of carbon dioxide in the soil. This increase became marked after the first month from the time of seeding, and increased to a maximum just previous to or after the plants headed, after which there was a gradual decline.

2. Millet produced about the same increase in carbon dioxide as did oats, but the production of carbon dioxide by each millet plant was approximately half as much as the production by each oat plant. The most marked rise in the carbon-dioxide content of the soil occurred at a later period of growth in the case of the millet than in the case of the oats.

3. The cropped soil, after the crop was harvested, maintained a higher carbon-dioxide content than was found in the bare soil. This was due probably to the decomposition of plant roots left in the soil.

4. It would seem that increased plant activity (growth) is accompanied by increased carbon-dioxide production. This theory is supported by the fact that a relationship was shown between the carbon dioxide produced presumably by the crop, and the water transpired.

5. Fluctuations in the content of carbon dioxide in the bare soil were accompanied by similar fluctuations in the cropped soil only after the removal of the crop and before the crop had made much growth.

6. There appeared to be little relationship between the temperature of the soil at the time of sampling, and the carbon dioxide in the cropped soil or that assumed to be produced by the crop (determined by subtracting the carbon dioxide in the bare soil from that in the cropped soil).

7. In the bare soil the carbon dioxide was usually high during warm weather and low when the temperature decreased.

8. Very low atmospheric pressures were usually accompanied by an increase in the content of carbon dioxide in the bare soil.

9. The carbon dioxide produced presumably by the plant was about the same in soils having a high initial carbon-dioxide content as in those low in carbon dioxide, indicating the probability that plants and soil organisms act independently in producing carbon dioxide.

10. It is concluded from this work that the plant itself, and soil organisms, produce most of the carbon dioxide in the soil; that the plant often produces at the period of its most active growth many times as much carbon dioxide as is produced by soil organisms; and that the excess carbon dioxide in the soil growing a crop is due to respiratory activity of the plants rather than to the decay of root particles from the crop growing on the soil at the time of analysis.

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APPENDIX

TABLE 1. CARBON DIOXIDE (PER CENT BY VOLUME) IN CROPPED AND IN UNCROPPED SOIL (OATS, 1917)

Date of sampling	Temperature (centigrade)	Atmospheric pressure (inches)	Water added to maintain moisture content at 30 per cent (grams)	Carbon dioxide produced in		Difference (A—B)
				Cropped soil (A)	Uncropped soil (B)	
March 30	22.0°	29.06	....	0.285±.009	0.281±.006	0.004±.011
April 12	23.0°	28.78	....	0.909±.017	0.777±.014	0.132±.022
April 15	23.0°	28.98	1.75	0.526±.007	0.498±.009	0.028±.011
April 19	30.0°	29.22	2.75	0.741±.019	0.736±.003	0.005±.019
April 22	21.0°	29.12	3.00	0.698±.017	0.653±.004	0.045±.017
April 26	22.0°	29.06	4.50	0.813±.013	0.714±.008	0.099±.015
April 30	23.0°	29.02	3.75	0.737±.014	0.653±.007	0.084±.016
May 4	17.0°	29.15	2.50	0.640±.013	0.559±.007	0.081±.015
May 7	21.5°	29.16	5.75	0.943±.027	0.776±.009	0.167±.028
May 11	22.0°	28.82	7.25	0.931±.037	0.632±.006	0.299±.037
May 14	30.0°	28.88	11.00	1.422±.048	0.878±.015	0.544±.050
May 18	16.0°	29.00	16.75	1.166±.047	0.475±.006	0.691±.047
May 21	21.0°	29.05	14.00	1.034±.037	0.452±.003	0.582±.037
May 25	16.0°	28.78	11.25	1.307±.040	0.415±.004	0.892±.040
May 28	17.0°	28.77	14.50	1.297±.034	0.477±.002	0.820±.034
June 1	20.0°	29.07	20.25	2.031±.102	0.648±.007	1.383±.102
June 4	29.0°	29.27	15.75	1.708±.060	0.698±.011	1.010±.060
June 8	21.0°	28.88	23.75	1.982±.101	0.530±.002	1.452±.101
June 11	22.0°	29.10	20.75	1.365±.042	0.452±.005	0.913±.043
June 15	13.0°	29.07	27.00	1.292±.024	0.416±.002	0.876±.024
June 18	22.0°	29.17	20.50	1.315±.025	0.419±.007	0.896±.026
June 22	20.5°	29.15	31.25	1.809±.030	0.480±.009	1.329±.032
June 25	30.0°	29.55	27.00	1.412±.033	0.466±.007	0.946±.034
June 29	20.0°	28.91	39.50	1.846±.028	0.496±.003	1.350±.028
July 2	28.0°	28.92	24.00	1.778±.032	0.620±.008	1.158±.033
July 6	16.0°	29.16	....	0.799	0.393±.002	....
July 9	24.0°	28.95	25.00	1.614±.014	0.449±.008	1.165±.016
July 13	19.0°	28.92	20.00	1.699±.018	0.394±.001	1.305±.018
July 16	30.0°	29.14	16.00	1.781±.052	0.633±.007	1.148±.052
July 20	20.0°	29.24	7.50	1.111±.016	0.491±.005	0.620±.017
July 23	35.0°	29.05	8.00	1.595±.030	0.954±.015	0.641±.033
July 27	23.0°	28.99	6.00	1.261±.044	0.686±.007	0.575±.044
July 30	35.0°	28.93	3.50	1.475±.029	0.959±.007	0.516±.030
August 3	21.0°	29.07	6.00	1.040±.032	0.643±.007	0.397±.032
August 6	25.0°	29.22	3.50	1.028±.028	0.629±.007	0.399±.029
August 10	19.5°	29.05	1.50	0.706±.012	0.425±.003	0.281±.012
August 13	26.0°	29.21	2.75	0.876±.012	0.581±.005	0.295±.013
August 17	20.5°	29.00	1.25	0.781±.019	0.478±.003	0.303±.019
August 20	32.0°	28.97	....	0.909±.012	0.704±.002	0.205±.012
August 24	22.0°	28.71	....	0.765±.013	0.526±.007	0.239±.015

TABLE 1 (*concluded*)

Date of sampling	Temperature (centigrade)	Atmospheric pressure (inches)	Water added to maintain moisture content at 30 per cent (grams)	Carbon dioxide produced in Cropped soil (A)	Carbon dioxide produced in Uncropped soil (B)	Difference (A−B)
August 27	29.5°	29.20	....	0.729±.009	0.538±.005	0.191±.010
August 31	14.0°	29.37	....	0.345±.007	0.244±.001	0.101±.008
Sept. 3	25.0°	29.24	....	0.659±.015	0.488±.001	0.171±.015
Sept. 7	14.0°	29.23	....	0.376±.007	0.256±.003	0.120±.008
Sept. 10	14.5°	29.34	....	0.289±.004	0.195±.003	0.094±.005
Sept. 14	15.5°	29.41	....	0.385±.010	0.255±.007	0.130±.013
Sept. 17	25.0°	29.31	....	0.544±.008	0.378±.004	0.166±.009
Sept. 21	18.0°	29.06	....	0.554±.010	0.348±.005	0.206±.011
Sept. 24	24.0°	29.40	....	0.415±.003	0.266±.003	0.149±.004
Sept. 28	18.0°	28.93	....	0.495±.012	0.328±.003	0.167±.013
Oct. 5	16.0°	28.89	....	0.309±.010	0.211±.004	0.098±.011
Oct. 19	24.0°	28.92	....	0.404±.010	0.288±.006	0.116±.011
Nov. 2	17.0°	29.40	....	0.382±.008	0.259±.004	0.123±.009
Nov. 16	19.0°	29.08	....	0.424±.013	0.301±.016	0.123±.021
Nov. 30	17.0°	29.15	....	0.280±.008	0.192±.005	0.088±.010
Dec. 14	17.5°	28.69	....	0.356±.020	0.216±.007	0.140±.021

TABLE 2. CARBON DIOXIDE (PER CENT BY VOLUME) IN CROPPED AND IN UNCROPPED SOIL (OATS, 1918)

Date of sampling	Temperature (centigrade)	Atmospheric pressure (inches)	Water added to maintain moisture content at 30 per cent (grams)	Carbon dioxide produced in Cropped soil (A)	Carbon dioxide produced in Uncropped soil (B)	Difference (A−B)
Jan. 3	18.0°	29.24	....	0.373±.020	0.229±.005	0.144±.021
Jan. 16	18.5°	28.84	....	0.346±.014	0.162±.002	0.184±.014
Jan. 31	18.0°	29.32	....	0.315±.009	0.223±.006	0.092±.011
Feb. 7	20.0°	29.20	....	0.318±.010	0.226±.002	0.092±.010
Feb. 11	20.0°	28.98	....	0.340±.010	0.249±.009	0.091±.013
Feb. 14	22.5°	28.97	....	0.401±.010	0.255±.009	0.146±.013
Feb. 18	18.0°	29.68	....	0.370±.010	0.221±.006	0.149±.012
Feb. 21	20.0°	28.75	5.00	0.509±.014	0.258±.008	0.251±.016
Feb. 25	20.5°	28.83	3.75	0.445±.009	0.195±.006	0.250±.011
Feb. 28	20.0°	29.25	5.00	0.595±.010	0.240±.008	0.355±.012
March 4	16.0°	29.34	5.75	0.695±.016	0.236±.008	0.459±.018
March 7	20.0°	28.96	3.25	0.639±.017	0.295±.007	0.344±.018
March 11	16.0°	29.54	9.75	0.834±.010	0.236±.006	0.598±.020
March 14	20.0°	28.48	9.75	0.969±.029	0.226±.006	0.743±.029
March 18	18.0°	29.15	14.25	1.688±.027	0.285±.006	1.403±.028
March 21	25.0°	28.88	19.75	2.290±.060	0.471±.012	1.819±.062
March 25	18.0°	28.84	24.00	2.103±.030	0.259±.009	1.844±.031
March 28	21.0°	29.39	17.50	2.224±.055	0.319±.010	1.905±.056
April 1	21.0°	28.81	30.75	2.514±.039	0.331±.010	2.183±.041
April 4	20.0°	29.08	27.00	2.314±.033	0.318±.006	1.996±.034
April 8	19.0°	29.39	33.25	1.865±.025	0.170±.009	1.695±.026
April 11	20.5°	29.26	14.00	3.129±.033	0.188±.004	2.941±.034
April 15	20.5°	29.22	22.25	2.704±.072	0.320±.006	2.384±.072
April 18	24.0°	28.83	29.75	2.580±.085	0.311±.004	2.269±.085
April 22	21.0°	28.68	24.25	2.129±.089	0.211±.005	1.918±.089
April 25	23.5°	29.28	15.00	2.678±.056	0.303±.006	2.375±.057
April 29	22.5°	28.97	38.50	2.418±.040	0.236±.005	2.182±.041
May 2	23.5°	29.20	21.00	2.069±.046	0.211±.003	1.858±.046
May 6	23.0°	29.07	31.00	3.343±.029	0.389±.003	2.954±.029
May 9	27.0°	28.93	30.25	2.741±.041	0.345±.004	2.396±.041
May 13	23.0°	28.92	24.25	2.643±.045	0.296±.004	2.347±.045
May 16	27.5°	29.41	21.00	2.753±.071	0.266±.004	2.487±.071
May 20	22.0°	29.12	23.00	2.600±.081	0.276±.004	2.324±.081
May 23	24.0°	29.30	17.75	2.934±.044	0.295±.006	2.639±.044
May 27	21.5°	29.05	17.25	2.153±.065	0.259±.006	1.894±.065
May 30	23.5°	29.17	16.75	1.518±.018	0.264±.005	1.254±.018
June 3	20.5°	29.19	27.00	2.045±.011	0.344±.005	1.701±.012
June 6	22.5°	29.10	18.25	1.331±.015	0.299±.005	1.062±.015
June 10	17.5°	29.11	17.75	1.120±.017	0.199±.003	0.921±.017
June 13	21.5°	28.77	10.75	1.070±.017	0.220±.004	0.850±.018
June 17	19.5°	29.09	15.50	1.170±.007	0.271±.005	0.899±.009
June 20	24.0°	29.21	11.75	1.004±.009	0.249±.002	0.755±.009
June 24	14.0°	29.00	5.50	0.519±.007	0.140±.002	0.379±.007

TABLE 2 (*concluded*)

Date of sampling	Temperature (centigrade)	Atmospheric pressure (inches)	Water added to maintain moisture content at 30 per cent (grams)	Carbon dioxide produced in		Difference (A−B)
				Cropped soil (A)	Uncropped soil (B)	
June 27	28.0°	29.06	6.00	1.169±.019	0.396±.003	0.773±.019
July 1	20.5°	28.84	5.25	1.500±.041	0.369±.006	1.131±.041
July 4	28.5°	29.33	....	1.026±.014	0.336±.005	0.690±.015
July 8	17.0°	28.99	....	0.763±.040	0.215±.002	0.548±.040
July 11	21.5°	29.12	....	0.745±.024	0.295±.007	0.450±.025
July 15	19.0°	29.12	....	1.028±.018	0.333±.004	0.695±.019
July 18	30.0°	28.94	....	1.430±.040	0.578±.011	0.852±.042
July 22	23.0°	29.31	....	1.778±.004	0.750±.021	1.028±.021
July 25	30.0°	29.22	....	1.648±.035	0.895±.017	0.753±.039
July 29	24.0°	29.14	....	1.788±.001	0.920±.021	0.868±.021
August 1	30.0°	29.07	....	1.020±.038	0.580±.029	0.440±.048
August 5	21.0°	28.92	....	0.653±.006	0.375±.017	0.278±.018
August 8	35.0°	29.03	....	1.563±.013	0.920±.036	0.643±.038
August 12	23.5°	29.16	....	1.088±.028	0.665±.012	0.423±.030
August 14	28.0°	29.07	....	1.315±.007	0.790±.026	0.525±.027
August 15	31.0°	29.21	....	0.885±.024	0.525±.021	0.360±.032
August 16	32.0°	29.16	....	0.835±.016	0.505±.021	0.330±.026
August 17	29.5°	29.50	....	0.760±.021	0.478±.023	0.282±.031
August 19	26.5°	29.53	....	0.668±.006	0.400±.014	0.268±.015
August 21	33.0°	29.21	....	0.715±.026	0.430±.010	0.285±.028
August 22	33.0°	29.17	....	0.888±.013	0.588±.018	0.300±.022
August 23	33.0°	29.10	....	0.988±.004	0.633±.014	0.355±.015
August 24	34.0°	29.02	....	1.145±.005	0.695±.007	0.450±.009
August 26	30.5°	28.96	....	0.788±.016	0.468±.006	0.320±.018
August 27	30.0°	29.28	....	0.688±.006	0.448±.020	0.240±.021

TABLE 3. RELATION BETWEEN THE CARBON DIOXIDE IN THE CROPPED SOIL DURING THE PERIOD OF MOST ACTIVE PLANT GROWTH, AND THE WATER TRANSPIRED EACH WEEK (OATS, 1917)

Date	Water transpired (grams)	Total water transpired each week (grams) (A)	Cropped soil: Carbon dioxide (per cent) (B)	Cropped soil: Average carbon dioxide for the week (per cent) (C)	Uncropped soil: Carbon dioxide (per cent) (D)	Uncropped soil: Average carbon dioxide for the week (per cent) (E)	Difference in carbon dioxide C—E (F)	Per cent of carbon dioxide to each pound of water: F/A (G)	Per cent of carbon dioxide to each pound of water: C/A (H)
May 7....	5.75	13.00	0.943	0.937	0.776	0.704	0.233	0.018	0.072
May 11...	7.25		0.931		0.632				
May 14...	11.00	27.75	1.422	1.294	0.878	0.677	0.617	0.022	0.047
May 18...	16.75		1.166		0.475				
May 21...	14.00	25.25	1.034	1.174	0.452	0.434	0.740	0.029	0.046
May 25...	11.25		1.314		0.415				
May 28...	14.50	34.75	1.297	1.664	0.477	0.563	1.101	0.032	0.048
June 1....	20.25		2.031		0.648				
June 4....	15.75	39.50	1.708	1.845	0.698	0.614	1.231	0.031	0.047
June 8....	23.75		1.982		0.530				
June 11...	20.75	47.75	1.365	1.329	0.452	0.434	0.895	0.019	0.028
June 15...	27.00		1.292		0.416				
June 18...	20.50	51.75	1.315	1.562	0.419	0.450	1.112	0.021	0.030
June 22...	31.25		1.809		0.480				
June 25...	27.00	66.50	1.412	1.629	0.466	0.481	1.148	0.017	0.024
June 29...	39.50		1.846		0.496				
July 2....	24.00	......	1.778	......	0.620	0.507	....	....	....
July 6....	.....		.....		0.393				
July 9....	25.00	45.00	1.614	1.657	0.449	0.422	1.235	0.027	0.037
July 13...	20.00		1.699		0.394				
Mean								0.024 ±.0012	0.042 ±.0031
Standard deviation								0.0054 ±.0009	0.0136 ±.0022
Coefficient of variability								22.5 ±3.74	37.40 ±5.65

TABLE 4. RELATION BETWEEN THE CARBON DIOXIDE IN THE CROPPED SOIL DURING THE PERIOD OF MOST ACTIVE PLANT GROWTH, AND THE WATER TRANSPIRED EACH WEEK (OATS, 1918)

Date	Water transpired (grams)	Total water transpired each week (grams) (A)	Cropped soil: Carbon dioxide (per cent) (B)	Cropped soil: Average carbon dioxide for the week (per cent) (C)	Uncropped soil: Carbon dioxide (per cent) (D)	Uncropped soil: Average carbon dioxide for the week (per cent) (E)	Difference in carbon dioxide C−E (F)	Per cent of carbon dioxide to each pound of water: F/A (G)	Per cent of carbon dioxide to each pound of water: C/A (H)
March 4	5.75	9.00	0.695	0.667	0.236	0.266	0.401	0.045	0.074
March 7	3.25		0.639		0.295				
March 11	9.75	19.50	0.834	0.902	0.236	0.231	0.671	0.034	0.046
March 14	9.75		0.969		0.226				
March 18	14.25	34.00	1.688	1.989	0.285	0.378	1.611	0.047	0.059
March 21	19.75		2.290		0.471				
March 25	24.00	41.50	2.103	2.164	0.259	0.289	1.875	0.045	0.052
March 28	17.50		2.224		0.319				
April 1	30.75	57.75	2.514	2.414	0.331	0.325	2.089	0.036	0.042
April 4	27.00		2.314		0.318				
April 8	33.25	47.25	1.865	2.497	0.170	0.179	2.318	0.049	0.053
April 11	14.00		3.129		0.188				
April 15	22.25	52.00	2.704	2.642	0.320	0.316	2.326	0.045	0.051
April 18	29.75		2.580		0.311				
April 22	24.25	39.25	2.129	2.404	0.211	0.257	2.147	0.055	0.061
April 25	15.00		2.678		0.303				
April 29	38.50	59.50	2.418	2.244	0.236	0.224	2.020	0.034	0.038
May 2	21.00		2.069		0.211				
May 6	31.00	61.25	3.343	3.042	0.389	0.367	2.675	0.044	0.050
May 9	30.25		2.741		0.345				
							Mean	0.043 ±.0014	0.053 ±.0022
							Standard deviation	0.0065 ±.0010	0.0102 ±.0015
							Coefficient of variability	15.1 ±2.32	19.17 ±3.12

TABLE 5. RELATION BETWEEN THE DRY WEIGHT OF THE CROP AND THE CARBON DIOXIDE GIVEN OFF BY PLANT ROOTS

(From Stoklasa and Ernest, 1909)

Crop	Total dry matter produced in 84 days (milligrams)	Total carbon dioxide produced in 84 days (milligrams)	Milligrams of carbon dioxide produced to each milligram of dry matter
Barley	34,493	1,267	0.037
Rye	27,046	1,053	0.039
Oats	26,215	793	0.030
Wheat	18,375	784	0.043
Average	26,532	974	0.037

TABLE 6. CARBON DIOXIDE (PER CENT BY VOLUME) IN CROPPED AND IN UNCROPPED SOIL (MILLET, 1918)

Date of sampling	Carbon dioxide produced in			
	Series 1 (high CO_2 soil)		Series 2 (low CO_2 soil)	
	Cropped (per cent)	Bare (per cent)	Cropped (per cent)	Bare (per cent)
July 8	0.713±.016	0.763±.040	0.210±.002	0.215±.002
July 11	0.763±.006	0.745±.024	0.283±.001	0.295±.007
July 15	1.045±.031	1.028±.018	0.358±.001	0.333±.004
July 18	1.455±.050	1.430±.040	0.578±.001	0.578±.001
July 22	1.803±.032	1.778±.004	0.795±.014	0.750±.021
July 25	2.015±.079	1.648±.035	0.908±.059	0.895±.017
July 29	1.923±.101	1.788±.001	1.008±.054	0.920±.021
August 1	1.305±.055	1.020±.038	0.798±.039	0.580±.029
August 5	1.133±.006	0.653±.006	0.750±.052	0.375±.017
August 8	2.115±.017	1.563±.013	1.628±.161	0.920±.036
August 12	2.025±.021	1.088±.028	1.223±.018	0.665±.012
August 14	2.448±.028	1.315±.007	1.710±.043	0.790±.026
August 15	1.864±.016	0.885±.024	1.405±.012	0.525±.021
August 16	1.950±.010	0.835±.016	1.480±.033	0.505±.021
August 17	2.108±.018	0.760±.021	1.683±.049	0.478±.023
August 19	2.040±.048	0.668±.006	1.683±.042	0.400±.014
August 21	2.288±.016	0.715±.026	1.948±.016	0.430±.010
August 22	3.098±.023	0.888±.013	2.655±.055	0.588±.018
August 23	3.095±.060	0.988±.004	2.715±.074	0.633±.014
August 24	3.345±.035	1.145±.005	2.690±.060	0.695±.007
August 25	2.465±.005	0.788±.016	2.275±.064	0.468±.006
August 27	2.198±.009	0.688±.006	2.133±.075	0.448±.020
August 28	2.245±.031	0.690±.036	1.958±.056	0.348±.004
August 29	2.093±.039	0.613±.004	2.120±.088	0.358±.006
August 31	1.983±.011	0.590±.007	2.245±.114	0.370±.010
September 3	1.770±.021	0.533±.011	2.143±.068	0.310±.005

TABLE 7. CARBON DIOXIDE (PER CENT BY VOLUME) IN CROPPED AND IN UNCROPPED SOILS HAVING DIFFERENT INITIAL CARBON-DIOXIDE CONTENTS (MILLET, 1918)

Date of sampling	Carbon dioxide produced in				Difference in carbon dioxide produced by various soils				
	High CO_2 soil		Low CO_2 soil						
	Cropped (A)	Bare (B)	Cropped (C)	Bare (D)	I (A—C)	II (B—D)	III (A—B)	IV (C—D)	V (III—IV)
July 8	0.713±.016	0.763±.010	0.210±.002	0.215±.002	+0.503±.016	+0.518±.010	—0.050±.013	—0.005±.003	—0.045±.043
July 11	0.763±.006	0.745±.024	0.283±.001	0.295±.007	+0.480±.006	+0.450±.025	+0.018±.025	—0.012±.007	+0.030±.026
July 15	1.015±.031	1.028±.018	0.358±.001	0.333±.004	+0.687±.031	+0.695±.019	+0.017±.036	+0.025±.004	—0.008±.036
July 18	1.455±.050	1.430±.040	0.578±.001	0.578±.001	+0.877±.051	+0.852±.012	+0.025±.064	0.000±.016	+0.025±.066
July 22	1.803±.032	1.778±.004	0.795±.014	0.750±.021	+1.008±.035	+1.028±.021	+0.025±.032	+0.045±.025	—0.020±.041
July 25	2.015±.079	1.648±.035	0.908±.059	0.895±.017	+1.107±.099	+0.753±.039	+0.367±.086	+0.013±.061	+0.354±.106
July 29	1.923±.101	1.788±.001	1.008±.054	0.920±.021	+0.915±.114	+0.868±.021	+0.135±.101	+0.088±.058	+0.047±.116
August 1	1.305±.055	1.020±.038	0.798±.039	0.580±.029	+0.507±.067	+0.440±.048	+0.285±.067	+0.218±.049	+0.067±.082
August 5	1.133±.006	0.653±.006	0.750±.052	0.375±.017	+0.383±.052	+0.278±.018	+0.480±.008	+0.375±.055	+0.105±.055
August 8	2.115±.017	1.563±.013	1.628±.161	0.920±.036	+0.487±.162	+0.643±.038	+0.552±.021	+0.708±.170	—0.156±.167
August 12	2.025±.021	1.088±.028	1.223±.018	0.665±.012	+0.802±.028	+0.423±.030	+0.937±.035	+0.558±.022	+0.379±.041
August 14	2.448±.028	1.315±.007	1.710±.043	0.790±.026	+0.738±.051	+0.525±.027	+1.133±.029	+0.920±.050	+0.213±.058
August 15	1.864±.016	0.885±.024	1.405±.012	0.525±.021	+0.459±.035	+0.360±.032	+0.979±.041	+0.880±.024	+0.103±.048
August 16	1.950±.010	0.835±.016	1.480±.033	0.505±.021	+0.470±.034	+0.330±.026	+1.115±.019	+0.975±.039	+0.140±.047
August 17	2.108±.018	0.760±.021	1.683±.049	0.478±.023	+0.425±.052	+0.282±.031	+1.348±.028	+1.205±.054	+0.143±.061
August 19	2.040±.048	0.668±.006	1.683±.042	0.400±.014	+0.357±.065	+0.268±.015	+1.372±.048	+1.283±.044	+0.089±.066
August 21	2.288±.016	0.715±.026	1.948±.016	0.430±.010	+0.340±.023	+0.285±.028	+1.573±.031	+1.518±.019	+0.055±.036
August 22	3.098±.023	0.888±.013	2.655±.055	0.588±.018	+0.443±.060	+0.300±.022	+2.210±.026	+2.067±.058	+0.143±.064
August 23	3.095±.060	0.988±.004	2.715±.074	0.633±.014	+0.380±.095	+0.355±.015	+2.107±.062	+2.082±.075	+0.025±.096
August 24	3.345±.035	1.145±.005	2.690±.060	0.695±.007	+0.655±.062	+0.450±.009	+2.200±.018	+1.995±.060	+0.205±.063
August 26	2.465±.005	0.788±.016	2.275±.064	0.468±.006	+0.190±.064	+0.320±.018	+1.677±.018	+1.807±.064	—0.130±.067
August 27	2.198±.009	0.688±.006	2.133±.075	0.448±.020	+0.065±.075	+0.240±.021	+1.510±.011	+1.685±.077	—0.175±.078
August 28	2.245±.031	0.690±.036	1.958±.056	0.348±.004	+0.287±.061	+0.342±.036	+1.555±.048	+1.610±.056	—0.055±.074

TABLE 8. CARBON DIOXIDE (PER CENT BY VOLUME) PRODUCED APPARENTLY BY THE MILLET CROP, 1918. DETERMINED BY SUBTRACTING THE AMOUNT OF CARBON DIOXIDE IN THE BARE SOIL FROM THAT IN THE CROPPED SOIL

Date of sampling	Carbon dioxide apparently produced by millet crop in		Difference (I—II)
	High CO_2 soil (I)	Low CO_2 soil (II)	
July 8	—0.050±.043	—0.005±.003	—0.045±.043
July 11	+0.018±.025	—0.012±.007	+0.030±.026
July 15	+0.017±.036	+0.025±.004	—0.008±.036
July 18	+0.025±.064	0.000±.016	+0.025±.066
July 22	+0.025±.032	+0.045±.025	—0.020±.041
July 25	+0.367±.086	+0.013±.061	+0.354±.106
July 29	+0.135±.101	+0.088±.058	+0.047±.116
August 1	+0.235±.067	+0.218±.049	+0.017±.082
August 5	+0.480±.008	+0.375±.055	+0.105±.055
August 8	+0.552±.021	+0.708±.170	—0.156±.167
August 12	+0.937±.035	+0.558±.022	+0.379±.041
August 14	+1.133±.029	+0.920±.050	+0.213±.058
August 15	+0.979±.041	+0.880±.024	+0.103±.048
August 16	+1.115±.019	+0.975±.039	+0.140±.047
August 17	+1.348±.028	+1.205±.054	+0.143±.061
August 19	+1.372±.048	+1.283±.044	+0.089±.066
August 21	+1.573±.031	+1.518±.019	+0.055±.036
August 22	+2.210±.026	+2.067±.058	+0.143±.064
August 23	+2.107±.062	+2.082±.075	+0.025±.096
August 24	+2.200±.018	+1.995±.060	+0.205±.063
August 25	+1.677±.018	+1.807±.064	—0.130±.067
August 27	+1.510±.011	+1.685±.077	—0.175±.078
August 28	+1.555±.048	+1.610±.056	—0.055±.074

TABLE 9. CARBON DIOXIDE (PER CENT BY VOLUME) IN CROPPED AND IN UNCROPPED SOIL OF LOW INITIAL CARBON-DIOXIDE CONTENT (MILLET, 1918)

Date of sampling	Temperature (centigrade)	Atmospheric pressure (inches)	Carbon dioxide produced in		Difference (I—II)
			Cropped soil (I)	Uncropped soil (II)	
July 8.....	17.0°	28.99	0.210±.002	0.215±.002	—0.005±.003
July 11....	21.5°	29.12	0.283±.001	0.295±.007	—0.012±.007
July 15....	19.0°	29.12	0.358±.001	0.333±.004	+0.025±.004
July 18....	30.0°	28.94	0.578±.001	0.578±.001	0.000±.016
July 22....	23.0°	29.31	0.795±.014	0.750±.021	+0.045±.025
July 25....	30.0°	29.22	0.908±.059	0.895±.017	+0.013±.061
July 29....	24.0°	29.14	1.008±.054	0.920±.021	+0.088±.058
August 1...	30.0°	29.07	0.798±.039	0.580±.029	+0.218±.049
August 5...	21.0°	28.92	0.750±.052	0.375±.017	+0.375±.055
August 8...	35.0°	29.03	1.628±.161	0.920±.036	+0.708±.170
August 12..	23.5°	29.16	1.223±.018	0.665±.012	+0.558±.022
August 14..	28.0°	29.07	1.710±.043	0.790±.026	+0.920±.050
August 15..	31.0°	29.21	1.405±.012	0.525±.021	+0.880±.024
August 16..	32.0°	29.16	1.480±.033	0.505±.021	+0.975±.039
August 17..	29.5°	29.50	1.683±.049	0.478±.023	+1.205±.054
August 19..	26.5°	29.53	1.683±.042	0.400±.014	+1.283±.004
August 21..	33.0°	29.21	1.948±.016	0.430±.010	+1.518±.019
August 22..	33.0°	29.17	2.655±.055	0.588±.018	+2.067±.058
August 23..	33.0°	29.10	2.715±.074	0.633±.014	+2.082±.075
August 24..	34.0°	29.02	2.690±.060	0.695±.007	+1.995±.060
August 26..	30.5°	28.96	2.275±.064	0.468±.006	+1.807±.064

Memoir 29, *The Lecithin Content of Butter and Its Possible Relationship to the Fishy Flavor*, the third preceding number in this series of publications, was mailed on December 23, 1919.

AY, 1920 MEMOIR 33

CORNELL UNIVERSITY
AGRICULTURAL EXPERIMENT STATION

THE RIBBED PINE-BORER

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THE RIBBED PINE-BORER

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THE RIBBED PINE-BORER

THE RIBBED PINE-BORER[1]

Rhagium lineatum Oliv.

WALTER N. HESS

Order, *Coleoptera* Family, *Cerambycidae*

The ribbed pine-borer (*Rhagium lineatum* Oliv.) is one of the commonest and most widely distributed species of cerambycids in North America. It is especially abundant in the vicinity of central Pennsylvania and about Ithaca, New York, where this study was conducted. Since these insects are very abundant and the limited literature concerning them contains little information regarding their life history, it has seemed advisable to make a more careful study of their habits.

A number of authors have briefly discussed the economic importance of the insect. Their reports, however, are conflicting and indefinite.

HISTORY OF THE SPECIES

The ribbed pine-borer, originally described by Olivier in 1795, has subsequently been briefly referred to by many authors. Kirby (1837) reports the insect from latitude 54°, and also from Massachusetts. Harris (1842) found the larvae of the species living between the bark and the wood of pitch pine. He states that they attack living trees, often extensively loosening the bark, which falls off in large flakes as a result and the trees die. LeConte (1850) states that the insects are found from Maine to Chihuahua, Mexico.

Rathvon (1862) describes the larva as a whitish grub about an inch long. He found larvae in large numbers just underneath the bark of trees, which they caused to fall off in large pieces, frequently resulting in the death of the trees. Packard (1883) reports the larvae as very common under the bark of pines that have been cut down for a year or more. He found the chief injury to consist in the loosening of the bark, which forwards the decay of dead timber. Hopkins (1899) found the insects to be very common bark borers, mining under the bark

[1] The author is indebted to Professor Glenn W. Herrick and Dr. Robert Matheson, of the Department of Entomology at Cornell University, under whose direction this study was made.

of dying and dead pine trees. He records the presence of larvae on July 14, pupae in October, and adults on April 8, May 5 and 9, October 17, and December 19.

Felt (1906) thinks these insects should not be considered injurious to living trees, as they live in rotten wood. Their operations, together with those of associated insects, soon loosen the bark so that it falls off in large sheets. Felt found the grubs transforming to adults during the latter part of the summer, in specially constructed pupal cells underneath the bark.

SYNONYMY

The ribbed pine-borer belongs to the order Coleoptera, family Cerambycidae, subfamily Cerambycinae, genus Rhagium, species *lineatum*. This species was first described by Olivier (1795) as *Stenocorus lineatus*, but was later placed in the genus Rhagium. Several workers, chiefly European, consider this insect the American form of the European species *inquisitor*, and hence give it varietal rank under this species as *Rhagium inquisitor lineatum* Oliv. There seems to be good reason for considering this species the same as the European *inquisitor*; however, since American workers list the American form as a distinct species, it is so considered in this discussion.

DISTRIBUTION

The ribbed pine-borer is commonly and widely distributed throughout the greater part of North America. It has been reported from twelve States in this country, in addition to Chihuahua (Mexico), Vancouver, and the Mackenzie River region of Canada. The States from which it has been reported are Maine, Massachusetts, New York, Pennsylvania, Virginia, North Carolina, Maryland, Louisiana, Michigan, New Mexico, Idaho, and Oregon. From these data it seems probable that the beetle ranges in distribution from northern Mexico to central Canada, extending across the continent from coast to coast wherever pine is found.

The species *inquisitor*, with which this species is often grouped, is widely distributed in the Old World. It has been reported from Europe, Siberia, Syria, and Japan.

HOSTS

All of the common species of pine in New York and Pennsylvania are attacked by the ribbed pine-borer. The species most commonly found

infested are the white pine (*Pinus strobus* L.), the pitch pine (*Pinus rigida* Mill.), and the red pine (*Pinus resinosa* Ait.).

These insects are usually reported as pine insects, and it seems probable that they attack all or nearly all species of pines throughout the United States and southern Canada. The writer has never found them infesting other conifers, such as larch and spruce, though it is possible that they may attack these at times.

METHODS OF BREEDING

Numerous attempts were made by the writer to determine the molts of this insect, but with little success. For this purpose pieces of bark were taken to the college insectary, cavities were made on the inner side of the bark, and larvae were placed in these cavities and covered with strips of celluloid as shown on Plate VIII, 5 and 6. The bark was kept in dark, moist jars, where it was easily accessible for examination. Though these larvae lived for many months in an apparently normal condition, they never reached maturity. For making shorter observations, such as that of the pupal stage, this process was very satisfactory.

LIFE HISTORY AND DESCRIPTIONS

The adult

This species, *Rhagium lineatum* Oliv., no doubt owes its specific name to the three smooth, rather strongly elevated, lines or ribs extending lengthwise along each elytron. The beetle is elongate, rather robust, and black mottled with reddish brown and gray. The greater part of its surface is covered with grayish hairs, giving it a grayish pubescent appearance.

The head, which is slightly narrowed behind the eyes, is attached to the thorax by a short neck. The antennae are short, scarcely reaching the bases of the elytra; they are not enveloped by the eyes but are inserted in front of and between them. The maxillary palpus is longer than the labial palpus; the last segment of each is bluntly pointed. The labrum is free. The eyes are oblong and slightly emarginate. The mandibles are flat, acute, and fringed on the inner margin.

The thorax is cylindrical, not margined, and much narrower than the elytra. It is armed on each side with an acute tubercle.

PLATE VIII

1. *Rhagium lineatum,* male

2. *Rhagium lineatum,* female

3. Larva of *Rhagium lineatum*

4. Pupa of *Rhagium lineatum*

5. Inner view of pine bark, showing celluloid strip underneath which are various stages of *Rhagium lineatum* larvae

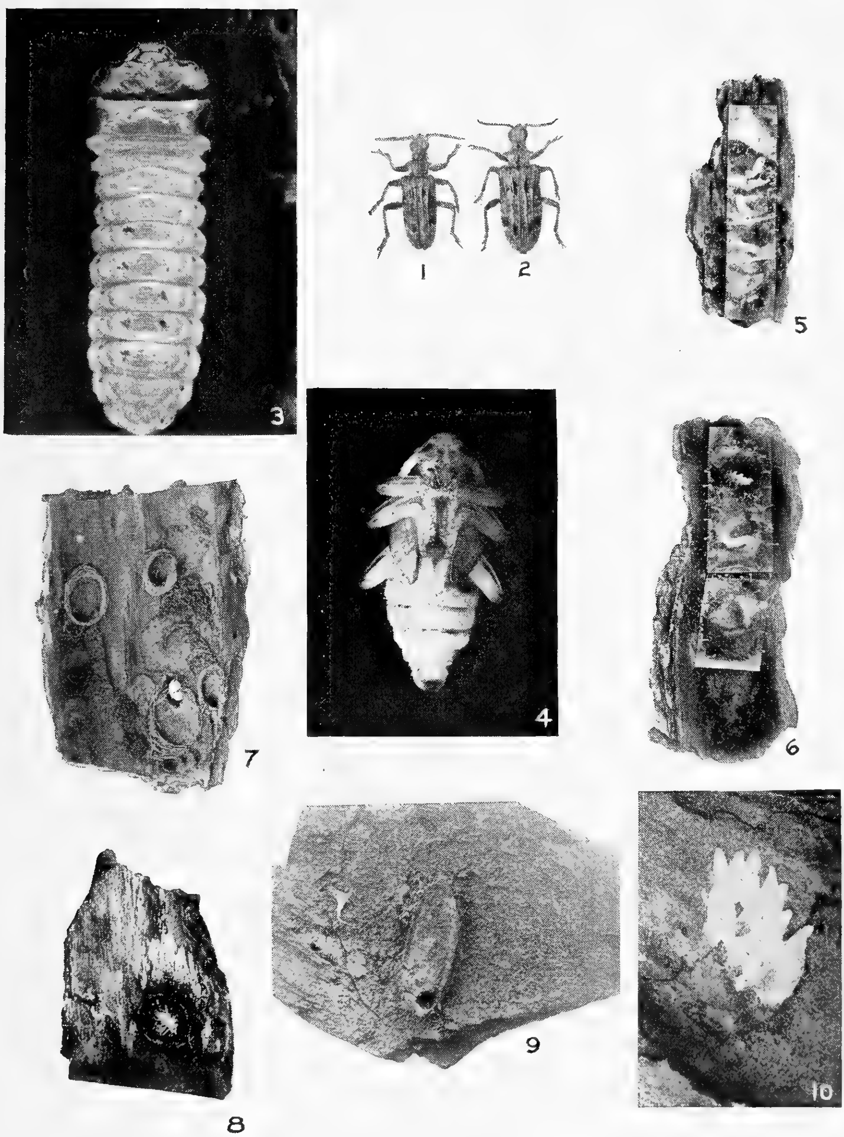
6. Inner view of pine bark, showing the arrangement of celluloid strips used in rearing larvae and pupae

7. Inner view of pine bark, showing four pupal cells. Photograph taken on April 8. The strips of wood woven into the frass in constructing the cells can be distinctly seen. The depressions at the sides of the pupal chambers were made by the adults in preparation for emergence. The lower cell shows a hole made by a woodpecker

8. Inner view of pine bark, showing in the pupal cell a larva of *Rhagium lineatum* which has been killed by a fungus

9. Pupal cell of an *Atanycolus simplex* which has parasitized a *Rhagium lineatum* larva. The exit hole of the parasite can be seen at the lower end of the pupal cell. The head of the parasitized larva is lying at the upper left side of the pupal cell

10. Egg mass on pine bark, exposed by removing a strip of the loose outer bark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The front coxae are conical and prominent; their cavities are open and are angulated externally. The front tibia has no oblique groove on the inner margin. The hind tibial spurs are terminal. The prosternum projects prominently between the coxae.

The elytra are gradually narrowed from about the middle to the apex. The intervals between the longitudinal ridges are coarsely and sparsely punctate.

The chief character that usually distinguishes this beetle is the extensive projection of the prosternum between the prominent fore coxae. Its general pubescence mottled with grayish brown and black, together with the short antennae, usually readily identifies this species.

The sexes are of the same general uniform coloration, but usually differ in two distinguishing characters: (1) the female (Plate VIII, 2) is about 3 millimeters longer and proportionally larger than the male (Plate VIII, 1); and (2) the tip of the abdomen is exposed in the female, while in the male it is entirely concealed by the elytra. The insects vary in length from 12 to 18 millimeters. Those found in small trees with thin bark, and hence scanty food, are usually smaller than those found in larger trees.

During the warm days of early spring the beetles become active in their pupal cells, and gradually begin gnawing through the bark to the exterior. The time of emergence is usually during the last week in April, but this may vary a week or more, depending on weather conditions. The beetles are active as soon as they emerge, and fly readily if disturbed.

Since these insects winter as adults the reproductive organs have had sufficient time to mature. In the spring the female's ovaries are full of large eggs. Copulation occurs as soon as the adults emerge. It occurs frequently, and a pair may remain in copula for several hours. In fact, during the first few days after emergence, this process may be repeated again and again at different times. One pair was taken in copula as late as the last week in June.

Although this beetle is a pine insect, and although it feeds on the bark after becoming an adult, it ceases to feed on pines after emerging. It then becomes a pollen feeder, feeding on such flowers as the dogwood — a habit which it has in common with many of its near relatives among the cerambycids.

The egg

When laid, the egg is pure white in color and is somewhat viscous, with a thin, fragile shell. It is ovoid in shape, being widest near the anterior end and tapering slightly toward the posterior. The shape, however, varies considerably, since owing to the softness of the shell it is easily modified by the shape of the crevice in which the egg is deposited. The entire surface is marked with very irregular elongate areas (fig. 61). The egg measures 1.9 millimeters long by 0.7 millimeter wide.

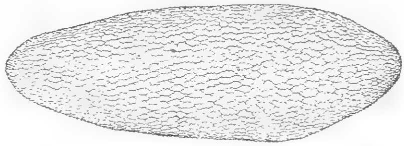

FIG. 61. EGG OF RHAGIUM LINEATUM, SHOWING MARKINGS

The egg stage lasts from eight to ten days, varying with weather conditions. In emerging, the young larva ruptures the egg in the lateral anterior region, usually on the right side. This it does by rubbing the sides of its head against the sides of the chorion, finally slitting the latter longitudinally. On each side of the head is a group of coarse setae which probably function in this process.

The larva

The newly hatched larva (fig. 62) is whitish in color and is slightly flattened. It is more rounded, however, than the mature larva, resembling rather the typical cerambycid type. The head and the thorax are slightly wider than the abdomen. The head is light brown in color, as are also the mouth parts except for the mandibles, which are dark brown toward the tips. At each side of the head is a group of coarse setae with dark brown chitinized basal parts, while scattered over the entire larva are a number of slender, elongate setae.

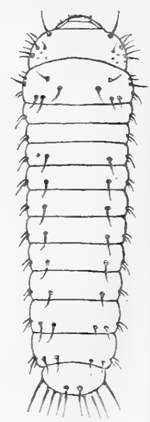

FIG. 62. FIRST INSTAR OF LARVA, DORSAL VIEW

Very soon after emergence, the newly hatched larva works its way through the outer bark into the cambium layer, where the larval life is spent. The larva at this stage is very delicate and soon perishes unless it reaches the cambium layer, where it begins at once to feed.

The mature larva (Plate VIII, 3) is long and is very much flattened, as a result of which it has been incorrectly called a flat-headed borer

(Kellogg, 1905). The head is very large and is slightly wider than the prothoracic segments. It has a triangular incision behind, the apex of which is met by a curved line passing back from the outside of the antennae and dividing the epicranium into two areas. The clypeus is short and wide. The labrum is about twice as wide as it is long, and is moderately rounded in front. The antennae are small and two-segmented, the second joint being blunt at the tip. The mandibles are large, with three cutting teeth. The maxillae are composed of only two segments besides the three-segmented palpus. The labium is large, with a prominent ligula which is slightly rounded at the front edge. The labial palpi are two-segmented.

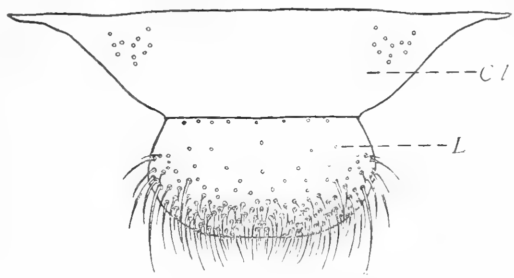

FIG. 63. CLYPEUS AND LABRUM, DORSAL VIEW

The prothorax is of about the same width as the other thoracic segments, but is more than twice as long. It has a flat, chitinized surface. The thoracic legs are slender and are composed of four segments.

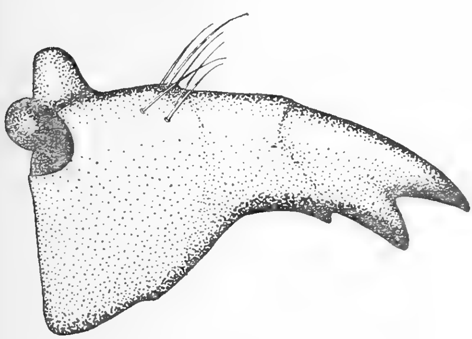

FIG. 64. LEFT MANDIBLE, DORSAL VIEW

The abdominal segments increase slightly in length posteriorly to the eighth, which is longer but narrower than the preceding ones. The ninth segment is of about the same length but is narrower than the eighth. The tenth is scarcely visible from above, being only about one-fourth as wide as the ninth; it is deeply cleft posteriorly.

The mature larva measures from 25 to 30 millimeters in length, with a maximum width of 6 millimeters in the region of the head and the prothorax. The width of the first abdominal segment is 5 millimeters.

This larva may undoubtedly be recognized by its habitat in the cambium of recently killed pine trees, by its relatively large size when mature, and by its broad, flattened head and body.

The mouth parts of the larva

Since these larvae closely resemble in appearance the flat-headed borers, the prothorax and the head are very wide and flat, resulting in a rather broad, short clypeus and labrum (fig. 63). The clypeus (Cl) is very wide at its basal part but tapers anteriorly to join the labrum. The labrum is about twice as wide as it is long, and bears on its dorsal side many long bristles and sense pits.

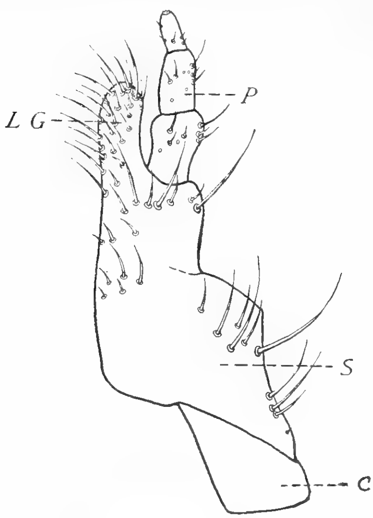

FIG. 65. MAXILLA, VENTRAL VIEW

C, cardo; S, stipes region; LG, undifferentiated lacinia and galea; P, palpus

The mandibles (fig. 64) are broad and heavily chitinized, and bear near the apices three rather sharp cutting teeth which fit them for both cutting and chewing.

The maxillae of the larva (fig. 65) are of a much simpler type than those of the adult. The cardo (C) is a distinct sclerite, triangular in shape. The stipes (S) and the lacinia and galea (LG) are not differentiated but are represented by one segment; near the apex on the inner margin are many long bristles, which probably represent the region of the future lacinia. The palpus (P) is three-segmented.

The labium (fig. 66) is large and covers the greater part of the lower side of the head. The submentum (SM) is broad and short. The mentum (M), while narrower than the submentum, is broad and flat. It bears the ligula (L), from which arise the two-segmented labial palpi (P). The greater part of the surface of the labium, but more especially the anterior edge of the ligula, bears numerous long bristles and sense pits.

The pupa

Pupation begins in the latter part of August and continues until late in October. Because of the varying temperature at that time of the year, the pupal period varies considerably. The individuals that pupated in August were found to emerge in from sixteen to twenty days, while those that pupated later took a month or even more to complete their pupal period. Some were found that wintered as pupae, but in every case observed these died before spring. When the adults emerge they are nearly white, and they require from two to five days to become fully colored.

The pupa (Plate VIII, 4) measures from 12 to 18 millimeters in length. It is white in color and rather convex in shape, and is without any special distinguishing markings. Scattered over its surface are many small setae, or spines.

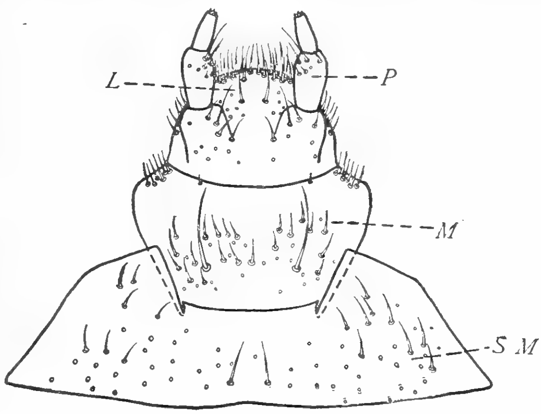

FIG. 66. LABIUM, VENTRAL VIEW
SM, submentum; M, mentum; L, ligula; P, palpus

HABITS

Of all the insects infesting the pine, few are commoner than, or as interesting to observe as, this species of cerambycid. Where the insects were studied in New York and Pennsylvania, they have been found during the winter months in large numbers, both as larvae and as adults, underneath the bark of white, red, and pitch pine. Here the larvae feed on the decaying tissues of the cambium layer.

The adults, which emerge in early spring, can be found during the last of May and in June on pines that have recently died. These insects always prefer the larger trees, and in this region the pitch pine is preferred to the other species, due possibly to the heavier bark which offers the insect more food and better protection. Trees less than six inches in diameter seldom, if ever, are infested with this insect; in fact, efforts have been made, by using cages, to have females oviposit on logs of this

size, with negative results. Where the insects have been found in trees of about this size, they frequently die before maturing, due probably to scanty food and to too little protection from cold and diseases. So far as is known, they never infest either trees that have been dead for more than three years or healthy living trees. They have been found in trees that had been injured by fire or other agencies on one side but were alive and healthy on the other side. The insects no doubt do material damage to such trees in hastening their death, not only by eating into the tissues that may be alive but also in opening and exposing the injured side to water and fungus attacks.

The normal time for these insects to oviposit on pine is in the spring following the death of the trees. The insects will oviposit on the trees again the second year, but only in rare instances will they do so the third year, and never the fourth year in so far as could be determined. In fact, by the third year the cambium layer is so nearly decayed that little is left for the larvae to feed upon.

The insects have been found from the very base of the stumps of the infested tree to near the top, where the trees were about six inches in diameter. They seldom are seen above this, and never in the limbs unless these happen to be very large. An idea of the number of individuals that may be found in an infested tree is given by notes made in regard to a tree cut on March 10, 1916. The tree was 16 inches in diameter at the base and was infested to a height of about 30 feet. It had been dead for two years, and so two broods were present. There were found 195 adults representing the first year's brood, and 155 larvae representing the second year's brood. These insects were rather uniformly distributed throughout the tree. In some cases they were as close together as two or three inches, while in other cases they were as much as a foot apart.

In badly infested trees the mines of these insects are more or less continuous by the end of the second or the third year, often separating the bark from the trees and not infrequently causing it to fall off. It is probable, however, that the burrows of other insects aid in this process.

Differing from most other cerambycid larvae, the larvae of this species move about comparatively little, but feed in all directions from a rather stationary point until all food within reach is consumed. They then move to one side or the other, leaving a large amount of frass behind them. Until the larvae are about three months old they make no special effort

to protect themselves from enemies. Toward fall, however, they construct about themselves a wall from débris, somewhat resembling that of the pupal cell. In the spring the larvae leave their winter cells for food, but during this second summer they usually keep themselves more or less protected by such a barrier. This they tear down and rebuild as they move about for food. As a result of this moving about, a rather extensive area, in the form of a blotch mine, is finally excavated.

During the early part of August of the second year the larvae prepare to pupate. This they do by enlarging and strengthening the chambers in which they have recently been feeding, forming what are called pupal cells (Plate VIII, 7). These cells are oval in shape, are about $\frac{1}{2}$ by $\frac{3}{4}$ inch in size, and lie just underneath the bark. They are constructed of frass which these or other insects have discarded, and are lined with strips of wood which the larvae tear from the bottom of the cells and push firmly into their walls. The excavation of the wood insures the insects plenty of room as well as a better protection against their enemies.

During late summer and early fall the second-year larvae transform to pupae, which in a period of from four to six weeks change to adults. They remain in the pupal cells over winter, emerging as adults the following spring.

SEASONAL HISTORY

Shortly after copulation, the female can be found on the bark of pine trees that have recently died. She walks over the bark, constantly searching with her ovipositor for crevices between the layers of the corky outer bark, in which she deposits her eggs in masses of from one to twenty-five or more, depending on the suitableness of the cavity (Plate VIII, 10). The writer found masses of eggs that hatched at different intervals, indicating that the insects may oviposit in the same cavity more than once.

Egg laying continues from about the middle of May until the last of June or the first of July. Since the eggs all mature at about the same time, the number laid by a single female can be easily ascertained. This number was found to vary from 120 to 165, indicating that the number is comparatively constant.

The eggs hatch into young larvae in from eight to ten days. As soon as they are hatched, they work their way through the bark, where they feed during their larval life on the tissues of the cambium layer.

Since this insect requires two years to complete its life cycle, the first winter is spent in the larval stage. From the time of hatching until late summer, the larva feeds freely in the cambium, but toward fall it constructs about itself a defensive wall of frass. In this condition it spends the winter. During the second summer the larvae usually keep themselves protected by such a defense, moving about only as they need a fresh supply of food. Unlike most larvae, they do not feed in definite channels, but move about irregularly, excavating a blotch-like mine which is often rather extensive.

Toward fall (about September) of the second year the larvae transform to pupae. About three weeks later they transform to adults. In this condition the insects pass the second winter. Toward spring the adults gradually gnaw their way through the bark, and emerge about the first of May. Though they feed very little before emerging, they eat a part of the bark as they bore their way to the exterior. They now no longer feed on the pine, but become pollen feeders like many other cerambycids. After emerging they soon copulate, and about the middle of May begin oviposition.

ECONOMIC IMPORTANCE

Rhagium lineatum, in the strict sense, can hardly be considered as an insect of economic importance in so far as any damage to living pines is concerned. Though its attack is limited to the region of the inner bark and the outer sapwood, it no doubt causes considerable damage to recently dead timber. Its excavations are usually extensive, and as a result the bark is frequently loosened, allowing moisture to enter. When water has once gained access, it is held by the large masses of frass. This is favorable for fungous growth, and hence the decay of the tree is hastened.

During the second and third years after the trees die, the exit holes made by the emerging adults admit large quantities of water, other insects, and fungi, by means of which the log is soon rendered useless for commercial purposes.

Natural control

In the control of the ribbed pine-borer, as in that of many other injurious species, nature has provided enemies which, under favorable conditions, are very effective in reducing their numbers. A wet season not only

makes it difficult for this insect to work, but develops fungi which attack all stages of the insect, especially the larvae (Plate VIII, 8). This is especially true in the case of trees with thin bark, for such trees are less resistant to moisture and the insects may become wet. Under such conditions the larvae, the pupae, and even the adults often die from fungus attacks. Those that survive until winter are often killed by frosts, which under such conditions are destructive to them.

The newly hatched larvae, while searching for an easy access to the inner bark, often expose themselves to predatory enemies which help in reducing their numbers. Birds, chiefly the woodpeckers, are probably the most important of these predatory enemies (Plate VIII, 7). It is not uncommon to find infested trees where these birds have removed from one-half to two-thirds of the larvae and adults during a single winter. Ants are usually common on the trees where the adult beetles are ovipositing. Though the insect tries to place her eggs in a secluded crevice, the newly emerged larvae often expose themselves. Ants have been observed carrying off both eggs and young larvae, chiefly the latter, as food.

Numerous centipedes, and larvae of staphylinids and carabids, are frequently found under the bark with the larvae of this insect, and may feed on them.

Though the insect constructs about itself a defensive wall, it seems probable that this wall is often ineffective against these enemies, especially in trees on which the bark has become loosened. Large carpenter ants have been found in the pupal cells of the ribbed pine-borer, but whether or not they are definitely harmful is not known.

A larval parasite, *Atanycolus simplex* Cresson,[2] which was reared from certain larvae, seemed fairly effective in reducing the numbers of this insect, especially farther south in Pennsylvania. In no case, however, were more than about five per cent of the larvae found infested. In New York this parasite is exceptionally rare, infesting only about one per cent of the larvae. When this parasite is mature it emerges from the larva and constructs a pupal cell underneath the bark (Plate VIII, 9). This occurs during the early fall. The adult emerges the following June. The remnants of the old Rhagium larva can often be seen attached to the pupal case of this parasite.

[2] Identified by S. A. Rohwer, of the Bureau of Entomology, Washington, D. C.

Artificial control

The insect can be artifically controlled by cutting all recently killed pines and removing the bark before the first of March. This will kill the larvae and the adults, and will do much to lessen attacks the following season. Where possible, the placing of newly felled logs in water will prevent attack. Putting logs in wet places will greatly reduce infestation, though it may hasten the decay of the timber. Repellents such as carbolineum, applied in May, will usually prevent oviposition.

A few years ago the ribbed pine-borer was exceptionally abundant about Ithaca; but during the past few years, due to the improved methods employed in this region by the Department of Forestry, at Cornell University, these insects, together with many of the more injurious forest insects, have nearly disappeared. This has been largely due to the practice of cutting and removing all trees as soon as they die or are found to be dying.

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THE CRANE-FLIES OF NEW YORK

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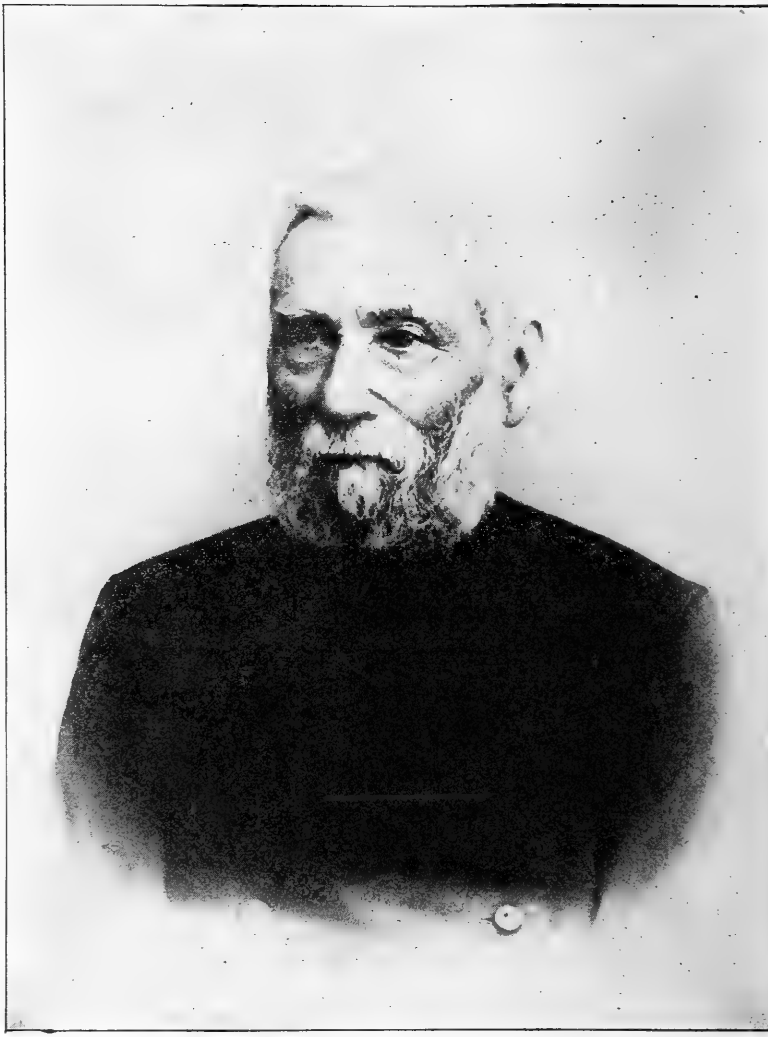

THEODOR BELING
(1816–1898)

KARL WILHELM THEODOR BELING

No sketch of the life of Theodor Beling, the great German student of the immature stages of the Tipuloidea, has ever appeared in English. It was with considerable difficulty that the writer was able to get into communication with relatives and friends of Beling and obtain the data presented herewith.*

Theodor Beling was born at Steterburg, in the Duchy of Brunswick, Germany, on March 26, 1816. He was a son of the district forester. From 1828 to 1834 he attended school at Wolfenbüttel. At Easter, 1834, he began his chosen career as a forester, having served his prescribed apprenticeship of two years with his father at Danndorf. He attended the Royal Saxon Academy at Tharand from 1836 to 1837, and in the following year visited the University of Göttingen to round out his technical training in various branches relating to forestry. Beling's career as a forester extends from Easter, 1834, to October 1, 1888, when he was officially retired with a pension. In April, 1861, he was made Master of the Forest, a position which he held until his retirement.

After his retirement from active public service, Beling long continued his vigorous researches afield and at home. When far advanced in years, he went alone on long trips to seek new stations for plants and to observe animal life in wood and field. He died on December 17, 1898, at Seesen, where much of his finest work was accomplished.

During his lifetime Beling published one hundred and seven articles. The series of three papers which rank him as a pioneer in the field of crane-fly biology were published in the years 1873, 1879, and 1886, respectively. In these papers the histories of sixty-nine species of crane-flies are discussed in detail, and brief notes on five additional species are included. The other published articles of Beling cover a remarkable range of subjects relating directly or indirectly to the science of forestry. His most important researches on the life histories of insects, in addition to those on the Tipuloidea, are on the coleopterous families Parnidae and Elateridae. His published articles are dated between 1850 and 1888, but practically all of his entomological studies were published in the seventies and eighties.

Beling's excellent collection of dried plants, mounted birds, and sections of various woods, and his cabinet of insects — the last-named including the types of several species described by himself and by others — are preserved in the collection of the Natural History Museum at Brunswick. It is understood that the insects in this collection, including the alcoholic larvae and pupae of the Tipuloidea, are still in excellent condition.

* Sincere thanks are here extended to the following persons, who have added materially to the value of this biographical notice:

Landesforstmeister K. Block, son-in-law of Beling, who published in April, 1899 (in *Allgemeinen Forst- und Jagd-Zeitung*), a complete obituary notice relating to his father-in-law, and to whom the writer is indebted for several additional unpublished notes and for the loan of the excellent portrait of Beling reproduced herewith.

J. Meerwartz, Director of the Natural History Museum at Brunswick, who has furnished data concerning the present condition of the collection of the immature stages of the Tipuloidea described by Beling, now preserved in the above-mentioned institution.

William Prindle Alexander and Elsa Müller Alexander, who have rendered valuable service in translating the account of Beling's life.

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THE CRANE-FLIES OF NEW YORK

PART II. BIOLOGY AND PHYLOGENY

THE CRANE-FLIES OF NEW YORK

PART II. BIOLOGY AND PHYLOGENY[1]

Charles Paul Alexander

A preliminary classification of the immature stages of the Tipulidae and related families, suggested to the writer by Dr. J. G. Needham in 1911, is presented in this memoir. But few of the sixty-odd families of Diptera, and comparatively few species of the Tipulidae, have as yet been studied from this viewpoint, and therefore the arrangement herein adopted must be considered as tentative. The majority of the specimens used in the study were reared in New York State, the crane-fly fauna of which is typical of a great area thruout northeastern North America. In 1913, thru the kindness of Dr. Charles D. Woods and Dr. Edith M. Patch, the writer was enabled to continue his investigations in Maine.

It is the writer's purpose to outline the morphological characters available for the classification of the larvae and the pupae, and to give preliminary keys for the separation of the various groups; such keys will, of necessity, require constant revision or complete remodeling with the accession of new life-history material, but it is at least hoped that they may furnish a basis for future investigation. The most important work on the European fauna, that of Theodor Beling (1873 to 1887),[2] is rendered incomplete by the total lack of illustration, the insufficiency of description of the details of the larval head, and the artificial nature of the keys. That this difficulty in using Beling's figureless descriptions is not confined to the writer is shown by the following criticism by one of his fellow-countrymen (Czizek, 1911:7):

> "Leider fehlen uns bis jetzt fast vollständig gute Abbildungen der Larven und Puppen, ein fühlbarer Mangel auch in Beling's Abhandlungen, da die genaueste Beschreibung das Bild nie ganz zu ersetzen vermag."

It is intended to include in this paper the following material:

1. Descriptions of all new life-history material available, with notes on the biology and occurrence of the species.

[1] Part I of *The Crane-Flies of New York*, dealing with distribution and taxonomy of the adult flies, was published in 1919 as Memoir 25 of the Cornell University Agricultural Experiment Station.

[2] Dates in parenthesis refer to *Bibliography and References Cited*, page 1019.

2. Brief summaries of published life histories of genera and important species not available for study as specimens and included here to complete the data.

3. Summaries and tabulations of life-history records, larval habitats, economic importance, and related subjects.

4. Keys to the families, tribes, and lesser groups.

The adult flies are not here considered in any detail, since they have been discussed by the writer in an earlier paper (Alexander, 1919 d).

The life histories remaining to be discovered in the Nearctic fauna are still numerous in species, tho few in genera. There are but four or five genera whose life histories when made known may upset the present ideas on arrangement. Until more is known of these missing groups, they must be classified according to the adult structure.

It will be noted that a number of important changes in nomenclature have been adopted in this paper. The system hitherto in vogue, based entirely on the structure of the imagines, was conceived by Osten Sacken and represented the culmination of research on the structure and affinities of the adult flies. A casual survey of the immature stages is sufficient to show the impossibility of many of the groups hitherto generally accepted. The principal modifications adopted in this paper are as follows:

1. The erection of the family Tanyderidae to receive the genera Tanyderus and Protoplasa. These had hitherto been placed with the Ptychopteridae, a group to which they are not closely allied.

2. The removal of the genus Trichocera from the Tipulidae to the Rhyphidae, and the inclusion of the latter family as one of the four existing families of crane-flies.

3. In the Tipulidae, the elimination of four tribes — Antochini, Limnophilini, Dolichopezini, and Ctenophorini — as being based on a conglomeration of forms referable to other tribes or else separated on an insufficient basis. The former tribe Antochini included members which the writer now refers to the Limnobiini (Antocha, Rhamphidia, Dicranoptycha, and other genera) and to the Eriopterini (Teucholabis, Elephantomyia); the Limnophilini are too close to the Hexatomini; and the tipuline forms constitute a very compact group which cannot well be subdivided into tribes.

4. The erection of nineteen subtribes, or divisions, to include lesser groups of genera within the tribes. In the following pages these are

treated in what seems to be their phylogenetic sequence from the generalized to the specialized.

The arrangement of families, subfamilies, and lesser groups may be summarized as follows:

Families	Subfamilies	Tribes	Subtribes	Representative genera
Eoptychopteridae (fossil)	....	....	....	Eoptychoptera
Architipulidae (fossil)	....	....	....	Architipula
Tanyderidae	....	....	....	Tanyderus, Protoplasa
Ptychopteridae	Ptychopterinae	....	....	Ptychoptera
	Bittacomorphinae	....	....	Bittacomorpha, Bittacomorphella
Rhyphidae	Rhyphinae	....	....	Rhyphus
	Mycetobiinae	....	....	Mycetobia
	Trichocerinae	....	....	Trichocera
Tipulidae	Limnobiinae	Limnobiini	Antocharia	Antocha
			Ellipteraria	Elliptera
			Limnobaria	Limnobia, Dicranomyia
			Dicranoptycharia	Dicranoptycha
			Rhamphidaria	Rhamphidia
		Hexatomini	Ularia	Ula
			Epiphragmaria	Epiphragma
			Pseudolimnophilaria	Pseudolimnophila
			Dactylolabaria	Dactylolabis
			Limnophilaria	Limnophila, Ulomorpha
			Hexatomaria	Eriocera, Hexatoma
			Polymeraria	Polymera
		Pediciini	Adelphomyaria	Adelphomyia
			Pedicaria	Pedicia, Dicranota
		Eriopterini	Eriopteraria	Erioptera, Ormosia
			Elephantomyaria	Elephantomyia
		Styringomyiini	....	Styringomyia
	Cylindrotominae	....	....	Cylindrotoma, Phalacrocera
	Tipulinae	Tipulini	Dolichopezaria	Dolichopeza, Brachypremna
			Ctenophoraria	Ctenophora, Tanyptera
			Tipularia	Tipula, Nephrotoma

A permanent series of the immature stages of the species studied has been carefully preserved in the writer's collection, while additional material has been placed in the principal collections of the United States. A series of two hundred and seventy microscope slides showing details of structure of the larvae and the pupae has been prepared, representing some seventy species arranged in forty genera. The typical larvae and pupae (*nepionotypes* and *neanotypes*) have been designated and preserved in alcohol for future reference.

For the most part, the life histories discussed in this paper have not been described hitherto. Besides the reared material, the writer has in his collection a very large number of unknown larvae and pupae, many of them representing interesting and undescribed types. In this paper but three or four of these are considered, and these only because they introduce new features of organization (Eriopterine No. 1, Tipulini No. 1 and No. 2).

A vast amount of work remains to be done on the immature stages of crane-flies. Exact, detailed life histories of individual genera and species are especially needed and the reward for effort will undoubtedly be great. Nothing is known of the tropical and the antipodal faunas, and their life histories will probably be unraveled but slowly, due to the inaccessibility of most of the regions.

The majority of specimens studied in the preparation of this paper were reared by the writer during the past nine years. Many specimens were received from various sources, however, including many of the most desirable life histories, and these are herewith gratefully acknowledged:

Dr. James G. Needham, Ithaca, New York. The extensive collections received from Dr. Needham include the material described in the various Adirondack reports, as well as numerous previously unrecorded specimens. In addition, the writer has accompanied Dr. Needham on many of his field trips in quest of the immature stages of aquatic insects, and has received much encouragement and inspiration from this association.

Charles W. Johnson, Boston, Massachusetts. Immature stages of Aeshnasoma, Elephantomyia, Teucholabis, and other species.

The late Frederick Knab, Washington, D. C. Immature stages of *Rhipidia bryanti*, Elephantomyia, *Epiphragma solatrix*, and other species.

J. A. Hyslop, Hagerstown, Maryland. Longurio (larvae), Oropeza, Gnophomyia.

J. R. Malloch, Urbana, Illinois. *Rhipidia bryanti.*

C. T. Greene, Washington, D. C. Protoplasa (supposition).

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William Lundbeck, Copenhagen, Denmark. Helobia and other species.

Dr. C. Wesenberg-Lund, Hilleröd, Denmark. Phalacrocera, *Ptychoptera paludosa*, *Tipula maxima*, and other species.

William G. Dietz, Hazleton, Pennsylvania. Notes on larvae of *Dicranomyia macateei* Alex.
Oskar A. Johannsen, Ithaca, New York. *Limnobia fallax,* and other species.
Carl Ilg, Philadelphia, Pennsylvania. Notes on *Rhipidia fidelis.*
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H. K. Munro, Pretoria, Transvaal. Notes on Trentepohlia and Styringomyia.
Charles Bruch, La Plata, Argentina. Notes on Trimicra, Helobia, and Epiphragma.
D. B. Young, Albany, New York. Notes on Gnophomyia.
J. T. Lloyd, Cincinnati, Ohio. Eriocera.
The late C. Gordon Hewitt, Ottawa, Canada. The Canadian-Arctic Tipulidae, including *Tipula arctica.*
A. E. Cameron, Ottawa, Canada. *Cylindrotoma splendens.*
R. C. Shannon, Ithaca, New York. Elephantomyia, Brachypremna, *Tipula fuliginosa,* and other species.
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The writer would express his great indebtedness to Dr. Ewald Bergroth, of Jämsä, Finland, for help in determining the derivation of some of the more obscure generic names in the Tipulidae; to Professor T. D. A. Cockerell for notes on the stratigraphy of fossil-bearing beds in many parts of the world; and to Miss Lela G. Gross, assistant editor of the Cornell memoirs, whose critical work on this and the preceding part under this title has been of the greatest value in assuring uniformity and accuracy.

Further acknowledgments of assistance in determining plant and animal associates of crane-flies are made thruout the text. In conclusion, the writer expresses his indebtedness to his wife, Mabel M. Alexander, for her untiring care and assistance in the typing and final preparation of this thesis.

GENERAL CONSIDERATIONS

REPRESENTATIVE CRANE-FLY LIFE HISTORIES

The life histories of but few species of crane-flies have been studied in detail. The very nature of the habitat (mud or earth) required by most species of the family renders it a most difficult operation to rear the species from the egg to the adult and note the various stages, their molts, their habits, and other features. The subfamily Cylindrotominae, the immature stages of which live on the leaves of various higher plants and curiously resemble the caterpillars of certain Lepidoptera, furnishes species whose habits are more readily studied than most others, and as a result the immature stages of this group are better known, perhaps, than those of any other section of the family. Two widely different species have been chosen, and their life histories as they are known at present are here outlined. The first is a species of Eriocera, a powerful, semi-aquatic carnivore; the second is a species of Cylindrotoma, a terrestrial herbivore. In the text which follows, notes on the life activities of various other species are given, but the gaps in the knowledge of this phase of the subject are very considerable and there still remain innumerable interesting facts to be ascertained.

Eriocera longicornis (Walk.)

The common crane-fly *Eriocera longicornis* is widely distributed over the northeastern United States and Canada. Altho the species is local in its distribution, the flies may be found in abundance wherever it does occur. The situations that favor the presence of these flies are large streams or rivers with sand or gravel bottoms and banks. The following notes were taken, partly in Fulton County, New York, along the Sacandaga River, and partly in Tompkins County, along Fall and Cascadilla Creeks. Some of these data have already been published by Alexander and Lloyd (1914:12–18) and by the writer (Alexander, 1915c:149–152).

On May 27, 1914, the adult flies were exceedingly numerous near the village of Northampton, Fulton County. They were present in untold myriads, and at every step they arose in clouds from under foot or from the leaves of chokecherry on which they rested. They sat on the leaves with the head directed away from the observer, ready to take instant flight, and at the first approach of a possible enemy they darted up into

the air and far overhead. A few were in copulation on the leaves, but from observations made later it seems probable that mating begins in the air and the united pair seek a support later on. Toward twilight the flies may be found in great numbers in company with many kinds of caddice flies and may flies. The swarms vary in numbers from about fifty individuals to those including many thousands. Some of the larger of these swarms cover a vertical height of at least fifty feet, the lower individuals being about fifteen feet above the water. When danger approaches, the swarm either mounts into the air overhead or retreats before the breeze, never advancing nor moving sidewise.

Out over the land in the smaller swarms, copulation was observed several times. The males in the swarm dart swiftly at the females and seize them almost instantly. They then usually leave the swarm and go sailing away, the male above doing the flying, the smaller female hanging limply beneath. The antennae of the male at this time are directed straight ahead and are slightly divergent, the legs hang downward, the wings vibrate rapidly. The female hangs downward with the legs trailing limply beneath, the wings nearly horizontal and motionless. The dead weight of the female continually pulls the male toward the water, and often both fall into the river. As a rule, copulation ends before the male is exhausted. The male opens his forceps and the female drops straight downward for a foot or so, quite like a parachute released from a balloon. If the pair are near the surface at the time of separation, the released female drops into the water. The male darts upward again and back into the swarm. The female slowly flies away, usually upstream but sometimes downstream, presumably to lay her eggs. She does not stop for swarms that she may encounter, and may even make a wide detour in order to avoid them. In a very few cases the female is the active partner and succeeds in pulling the male where she wills altho she is much smaller. No matings were observed during the hours of sunlight, and it was only at twilight or just after sunset that mating took place. Often a second male will seize a female already in copula and the three will come tumbling down into the water together. One such pairing of three individuals came down, and when they were about a foot above a board in the water the male in copulation dropped the other two. These rested for a moment, and then the remaining male attempted to engage the female in copulation. She resisted but finally he managed to seize her

with his forceps. Then he attempted to fly away, but she seized hold of the board with all her feet and he was unable to disengage her. This seems to indicate that the normal place for copulation is in the air.

The motions of the insects in the swarm were very rapid, almost like those of bees, and the sound produced was at a very low pitch, much lower than that made by Culex. The movements are on a horizontal plane, each individual flying mostly in the path of a figure 8, sometimes slowly and at other times much more rapidly.

Many specimens were seen dipping down into the water, as tho engaged in laying eggs. All of the few specimens captured proved to be males, but why this sex should go thru these motions is not clear to the writer. This action has been observed several times in various species of crane-flies. It is very probable that the female lays her eggs in the water in this manner.

The eggs are pale white or brown, not heavily chitinized as are those of Hexatoma but with the chorion feebly sculptured. They vary in number from 892 to 1034, with an average of 952. They are small, about the same size as those of Hexatoma. The ovaries almost completely fill the abdominal cavity, and the eggs are arranged in the ovaries like bananas on a stalk, with numerous pale nurse-cells in between.

The larval life is passed in streams, usually under rocks. The winter is spent in the larval condition, but the larvae do not attain full size until the following spring. At this time they come to the land and live in the sand and gravel along the banks of the streams. By the alternate extension and contraction of the body and the inflation of the penultimate segment of the abdomen at the moment of extension, the larvae are capable of inflating this segment into an enormous globular structure which serves as an aid to progression thru the soil. The food of the larvae consists largely of animal matter, and often large species, such as chironomid larvae, are swallowed whole. The almost total lack of chitinization of the mental region allows for great distension of this part of the body. The powerful mandibles and the retrorsely roughened esophagus serve the function of both holding the prey and preventing its ejection when once swallowed. Considerable gravel and particles of vegetable tissue are also found in the proventricular region.

When ready to transform to the pupal condition, the larva becomes sluggish. After molting the last larval skin, the pupa is disclosed, pale

yellowish white and very callow. The pupa forms burrows in the loose gravel, these being vertical, or, more often, a little oblique. The diameter of the burrow is a little greater than that of the pupa. The length varies, the burrow for a young pupa being a mere chamber inclosing the individual and located from one-half to one inch below the surface. As the pupa becomes older, by a bobbing up-and-down motion it lengthens the burrow upward until finally it penetrates the surface layer and forms a small shot-like opening. Here the pupa rests, often bobbing up and down with a rhythmic motion, but ducking down into the burrow when danger threatens. The length of the burrow is rarely more, but usually less, than twice the length of the pupa. A few of the pupae seem to be inclosed in a very delicate silken tube and the salivary glands seem to be well adapted for the purpose of forming silk; but the great majority of the pupae are entirely naked. The indoor pupal period varies from one hundred and seventy to one hundred and seventy-three hours, or a little more than seven days. The outdoor pupal period, however, is undoubtedly longer, unless the weather is very warm.

The emergence of the adults usually takes place during the late hours of the morning, the greatest number emerging between ten o'clock and noon. When ready to emerge, the pupa pushes part of its body out of the earth, the posterior two-thirds or half remaining attached to the soil. If it projects farther than this, its transformation seems to be a very difficult operation. The pupa bends backward and forward constantly, flexing the body dorso-ventrally. This motion appears to exhaust it, since it frequently rests. The skin splits lengthwise up the mesonotum and the adult emerges. The male has difficulty in extricating its very long antennae from their sheaths. The tips of the fore femora are placed underneath the sharp spines of the flagellum, and by raising the legs the insect pulls the antennae slightly outward. These spines are regularly spaced, and, since both fore legs work in unison, the spines function as cogs and the whole antenna is gradually forced from the pupal sheath. The body is carried very straight and stiff during the operation, and the abdomen is very long and pale. The drawing out of the extreme tips of the antennae is usually accomplished by the insect flexing its whole body backward. When the antennae are freed, the insect walks a few steps from the cast skin, withdrawing its abdomen from the case. (The emergence of *E. spinosa* is shown in Plate XII, 1.) A drop of nearly colorless liquid is excreted

from the body at this time. The teneral adult then waits quietly until it gains more strength and color. This condition of the insect is the most dangerous period of its existence, since it is defenseless against all enemies.

The insects are associated in the gravel with ground beetles of the genera Omophron, Schizogenius, Dyschirius, Bembidion, Tachistodes; with click beetles of the genus Cryptohypnus; and with rove beetles, of which Paederus, Lathrobium, and Gastrolobium are the commonest forms. In addition, numbers of larvae of Tabanidae, Leptidae (Atherix), *Eriocera spinosa, E. fultonensis, E. cinerea,* and *Erioptera armata* were found. Natural enemies of the pupae and the teneral imagines are the medium-sized black lycosid spiders, which preyed in numbers on the weak, uncolored adults. Dozens of these spiders were noticed with individuals of the crane-flies in their grasp. When alarmed they would run rapidly away, but only in exceptional cases would they release their victims. A few spiders of other families, notably the Attidae, were found with Eriocerae. Dragon-flies appear to be the most serious enemies of the active adults. *Helocordulia uhleri* (Selys) has been observed capturing the crane-flies by darting back and forth thru the swarms of individuals.

Cylindrotoma splendens Doane

The life history of the species *Cylindrotoma splendens* has been worked out in considerable detail by Dr. A. E. Cameron, from material obtained near Westholme, Vancouver Island, British Columbia, in late April, 1917. The following account is abstracted from Cameron's detailed paper (1918) on this interesting crane-fly:

The adults first appear on the wing about the middle of May. Without food they do not live longer than five or six days, but in breeding cages, where they were supplied with food in the nature of a sugar solution, they lived as long as from seven to nine days. In nature the adults were found on the wing during a period of about three weeks.

Soon after emergence the adults begin to copulate, and one male may have intercourse with more than one female. Copulation often takes place in a vertical position, the female above, the male below, with the tips of the abdomens interlocked. At times the female was noted hanging to the roof of the breeding cages, with the male suspended head downward, his body at an angle of 90° to that of the female, and his legs unsupported. If disturbed, the female may walk off, dragging her mate after her, or she may take flight, bearing the male with her. In nature the act of copulation is generally undertaken in the deep shade of the large leaves of the insect's food plants, the sexes resting on the under surface of the leaves or on the stems. Copulation may last but a few minutes or may require several hours.

The eggs are of a dull glistening white, elongate-oval in shape. Under natural conditions they are almost invariably found on the under surface of the leaves of the food plant *Trautvetteria grandis* Nuttall (Ranunculaceae), inserted beneath the incised epidermis. They

are usually deposited in series along and just within the margin of the serrate, palmately-lobed leaf. They are found in groups of one or more, all arranged parallel to one another and with their long axes perpendicular, or nearly so, to the margin of the leaf. The eggs are only partly hidden beneath the epidermis, being exposed dorsally, the margins of the slit overlapping the egg laterally and, to a lesser degree, both anteriorly and posteriorly. This arrangement of the eggs in series gives to the leaf margin a somewhat beaded appearance. When the eggs are older, the leaf margin turns brown and the presence of the eggs is readily detected. In ovipositing, the female rests on the under side of the leaf, with the tip of the abdomen directed toward the leaf edge. The abdomen is slightly flexed ventrally, and the margin of the leaf is held between the bifurcated valves of the ovipositor, which is applied to the upper surface of the leaf, while the paired cutting valves, with their blades, are applied against the under surface. These blades are then moved to and fro, cutting a slit in the epidermis. The eggs are then deposited. In no case do the eggs actually touch one another on the leaf. In the breeding cages females lay their eggs indiscriminately on both the upper and the lower surface of the leaves. In some cases, when a leaf has been eaten earlier in the season by larvae, the female will deposit her eggs along the ragged edge of this damaged part.

The indoor duration of the egg stage is from fourteen to eighteen days, but in the field as long a period as three weeks may be required. When first deposited the egg is translucent, grayish white, and spindle-shaped, with the chorion unornamented, and measures on an average 0.84 by 0.303 millimeter.

The larva requires about three hours to emerge from the egg. The chorion of the egg splits longitudinally down the mid-dorsal line, the slit extending almost half the length of the egg. In emerging, the almost transparent, grayish white larva utilizes the body tubercles as levers in freeing itself from the eggshell. As soon as it is freed from the shell, the newly hatched larva begins to feed on the leaf tissue of the host plant.

The first-stage larvae are grayish white in color, are translucent, and measure 1.19 by 0.37 millimeter in size. They feed on both the upper and the lower surface of the leaf, burrowing thru the epidermal layer with their mandibles and feeding on the parenchymatous tissue within. The young larvae are very sluggish and are not readily disturbed when feeding, the mandibles being firmly embedded in the leaf tissue. While engaged in feeding they assume various positions on the leaf surface. At the end of nine days the larvae have increased in length to 5.84 millimeters, and show all the characteristic behavior of the full-grown larvae. Growth is very slow, and before the first molt the larvae become covered with particles of their excrement, which adheres readily to the skin. The first larval molt occurs after a period of from eighteen to twenty-one days; in some cases, however, it does not occur until five or six weeks have elapsed.

The second-stage larvae gradually assume a leaf-green color as they continue to feed. Toward the end of July, coincident with the dying-off of their food plant, the larvae, which have now reached a length of from 8.32 to 9 millimeters, become quiescent and cease to feed. Feeding and movement gradually cease completely and the larvae remain clinging motionless to the leaves. As the leaves wither, the larvae drop off, and, in some cases, attach themselves to the stems; under natural conditions, however, they usually fall among the dead leaves on the ground and under these they pass the winter in a dormant condition. Many of these larvae match the brown color of the dead leaves, but some of them retain their leaf-green tint.

The overwintering larvae first show signs of activity in March of the following spring, when *Trautvetteria grandis* sends up its new shoots. Growth then proceeds rapidly until pupation in the middle of May. There seems to be one molt before hibernation and two after, the last being the casting of the larval skin, previous to pupation. The fully grown larvae measure 17 millimeters. They are invariably found on the upper surface of the leaf, and in the spring are actively engaged in feeding. On a fresh leaf the larvae usually begin by skeletonizing it, leaving the lower epidermis intact. Later on, however, large holes may be eaten completely thru the leaf. The fully grown larvae, and to a somewhat lesser degree the younger larvae, progress by a looping motion, which may be aptly compared to that

of the measuring worms (Geometridae), progression being accomplished by the aid of the mandibles and the ventral tubercles, or pseudopodia. In a quiescent condition the thoracic region of the body has a noticeable humped appearance. The fully grown larvae are very sluggish and inactive. When disturbed they relax their hold on the leaf surface and fall to the ground. Altho several hundred adults were reared, not a single parasite was discovered.

Before pupation the larva attaches itself firmly to the surface of the leaf or to the leaf petiole, by means of its anal pseudopodia. The skin splits transversely behind but is only partially sloughed off. The head, the thorax, and the first four abdominal segments of the pupa are exposed, but the apex of the abdomen remains encased in the larval skin, the terminal part of which, collapsed and wrinkled, is attached to the leaf surface. Pupation may take place on either the upper or the lower surface, but it occurs oftener on the former. If pupation takes place on the petiole, it is generally at the axil. In the breeding cages the duration of the pupal period was found to vary from six to ten days.

When the adult first emerges it is of a pale green color, which is gradually replaced by the black and yellow of the fully colored insect. From one and one-half to two hours are required for the adult to emerge. After emergence is completed, the fly rests for a short period until the cuticle hardens and the wings expand. It seems that the adherence of the larval skin to the pupa is necessary for the emergence of the adult, at least in many cases. There appears to be a large disproportion of females over males, this sometimes being as high as five to one. Since a single male may copulate with several females, this disproportion is not so serious as it appears at first sight.

LIFE ACTIVITIES OF CRANE-FLIES

The adult

Emergence.— Emergence from the pupal hull may require but a few seconds (as described for Gnophomyia by Hyslop *in litt.*, the whole operation requiring but eight seconds), or it may take several hours. The emergence of the strictly aquatic genus Antocha has not been observed, but it must be practically instantaneous as in Blepharocera and the lotic caddice flies.

Mating.— In several widely different species, the females as they emerge from the pupal hulls are at once seized in copulation by the males altho they are still callow and uncolored. Mik (1882 b:40, and 1886 a) discusses this curious condition in considerable detail. In all the cases that are known to the writer — *Dicranomyia trinotata, Discobola caesarea,* and *Cylindrotoma distinctissima* (Mik, 1886 a, the last-named also cited by Mik, 1882 b), *Liogma glabrata* (Müggenberg, 1901), *Tipula rufina* (Giard, 1895), and *Tipula ultima* (Caudell, 1913) — the abdomen of the female is elongate, flabby, and nearly colorless. In *Dicranomyia trinotata* the females scarcely have time to remove their legs from the pupal sheaths before they are seized in copulation. In other cases the males emerge before the females and wait beside the pupae for the emergence of their mates, when they at once seize them in copula. In most species of Tipula the males, when seeking the females, progress by a fluttering

motion, partly flying and partly walking, over the ground or up the trunks of trees. This habit is discussed under the account of *Tipula taughannock* (p. 1013), and has been observed in other woodland-inhabiting species of this genus — as *T. macrolabis*, *T. fuliginosa*, *T. fragilis*, and others. In *T. fragilis*, when a male comes upon a pair already in copula he passes on without interrupting them. Somewhat similar mating habits are found in some species of Dicranomyia (*D. trinotata*, *D. badia*, and *D. simulans*), Discobola, Antocha, Chionea, *Dactylolabis montana*, some Pediciini as Dicranota, and the Cylindrotominae.

Many crane-flies have developed swarming habits for the purpose of mating, these including representatives of most of the tribes of the Limnobiinae and a few tipuline forms. *Dicranomyia morioides* was observed by Needham (1908 a:204) swarming in vast numbers near Ithaca, New York, but here the swarms consisted only of males. Likewise, *Erioptera armata* (Needham, 1908 a:206) was found swarming near Lake Forest, Illinois; but, out of several hundred individuals captured, all except three were males. The writer has observed swarming in numerous species of Ormosia, Molophilus, Erioptera, Gonomyia, Rhabdomastix, Limnophila, Ula, Epiphragma, Eriocera, Dicranota, Rhaphidolabis, Trichocera, and other genera, and here, too, the males were always predominant. The specific data may be consulted under these various headings. The males of Dicranota swarm in rather large numbers preliminary to searching for the females, which rest quietly on the branches of neighboring shrubbery. *Limnophila ultima*, as noted at Gloversville, New York, on September 7, 1916, was swarming at half past six o'clock in the evening. The swarms here consisted of from fifty to sixty individuals and took place from ten to eighteen feet above the earth. Mating took place frequently in the air, and as soon as a pair were in copula they flew away to some point to rest, many pairs being observed hanging on a clothesline a few feet away. There were three distinct swarms, which showed little tendency to fuse altho their flight area was very close. The vast swarms of *Eriocera longicornis* and of Trichocera are mentioned or discussed elsewhere in this paper. When pairs are in copula, they readily take flight, still united, the female usually trailing the male after her; altho in a few groups, in which the male is the larger individual of the two, the situation is the opposite. Brachypremna, the familiar " weaver " of the Southern States, has a very remarkable vertical dance of several

feet in shady spots, and has been aptly termed by Johnson (1907–12 [1909]:123) " the king of the dancing tipulids." Doubtless many interesting facts remain to be discovered concerning the dances of the tropical species of Brachypremna, Tanypremna, and Megistocera.

Dancing.— The dances of *Thrypticomyia saltens* (Dol.) should be mentioned at this point. According to Doleschall (1857), Jacobson (De Meijere, 1911:22–23), and others, this species is common in Java in shady places thruout the year. The insects have the habit of clinging to spider webs by means of the fore feet, or, if a fore foot is lacking, one of the middle legs is used. Often twenty or more of these flies are seen hanging close beside one another on a horizontally spun web, all seesawing rapidly up and down and at the same time swaying to and fro, sometimes rhythmically, sometimes not. This ludicrous tight-rope dance is continued for a long time. Somewhat similar habits have been described for *Trentepohlia pennipes*, *Rhamphidia venustissima* Alex., and other species with white tarsi.

Bobbing.— Species of Dicranomyia and Geranomyia, as well as a few other crane-flies, have the curious habit of bobbing up and down while resting, the long, slender legs acting as springs. The species of the latter genus practice this same oscillating movement while resting on a head of flowers and feeding. H. K. Munro has recorded this bobbing habit in a species of Trentepohlia (p. 943).

Resting habits.— When at rest crane-flies assume various positions which are often fairly characteristic. Many species (Erioptera, Molophilus, and some Dicranomyia) resemble spiders when flattened against a tree trunk or some other vertical support. Styringomyia resembles a bit of cobweb, the fore and middle legs stretched out in front, the hind legs directed backward. In a position of rest the tipuline forms generally hold their wings outspread or divaricate, exceptions being in the genera Longurio, Oropeza, and others, and in a few species of Tipula, as *T. arctica* and the woodland-inhabiting species of the *marmorata* group (*T. fragilis* and *T. ignobilis*). The limnobiine forms usually fold the wings incumbent over the abdomen, but here again exceptions are found in Pedicia, *Limnophila toxoneura*, and other species, which normally rest with the wings outspread. Oropeza hangs to the roofs of bridges, culverts, and similar places, with only the fore legs attached to the support, the middle legs divergent, the posterior legs hanging loosely behind. The apparently

closely allied Dolichopeza, on the contrary, has the four anterior legs on the support, the hind legs dangling, the wings divaricate. Many of these species — as Oropeza, Dolichopeza, *Dicranomyia badia*, and exotic species of the genera Thrypticomyia and Trentepohlia — habitually rest on spider webs (page 982; also, Knab, 1912). During heavy rains, crane-flies rest on the lower side of the broad leaves of deciduous trees or hide beneath loose flakes of bark.

Feeding.— The adult flies feed but little, the majority of the species whose habits are at all known merely lapping nectar from open flowers. Knuth (1909:579) and Wahlgren (1917) record the plants frequented by a number of European Tipulinae as well as by Ptychoptera. These species are found on Umbelliferae (Aegopodium, Anthriscus, Heracleum, Carum, Anethum, and other genera), on Rosaceae (Spiraea, Rubus, and other genera), and on a few other plants. A few of the local Limnobiinae have the rostrum very greatly elongated — an obvious adaptation for sucking the nectar from tubular flowers. The species of Geranomyia feed on various composite, umbelliferous, and lauraceous flowers. Toxorhina frequents composite, rhamnaceous, apocynaceous, and ericaceous plants. The exact plants frequented are discussed under the descriptions of the respective genera.

Oviposition.— The females lay their eggs in the habitat frequented by the larvae. In the case of aquatic forms — as Antocha, Hexatoma, Eriocera, and other genera — the eggs are deposited in dipping down to the water surface, one or more eggs being deposited at each descent. Forms that live in mud or moist earth lay their eggs in these situations. Many species with acute ovipositors insert the eggs carefully into the soil or other substance. The oviposition of *Limnophila* (*Eutonia*) *alleni* as noted by the writer may be regarded as typical of this class of species:

Observations made at Gloversville, New York, June 28, 1916. A female was noted ovipositing in low, wet spots along a small woodland stream. She flew about slowly and silently, just skimming the ground, until a place suitable for egg-laying was found. She finally chose a much-decayed log and the eggs were driven home securely by the acicular tergal valves of the ovipositor. Much effort is expended to place the eggs firmly and the rate of oviposition is not more than eight or ten a minute, the female often pausing to rest for several seconds. While thus engaged, the fly is entirely unconcerned with other agencies and may be picked up by hand.

The females of most crane-flies usually live but a short time after egg-laying is completed. Indeed, the entire duration of life of the adult crane-flies is probably but a few weeks at the most.

The specialized methods of oviposition in the Cylindrotominae have already been discussed on page 709 under the account of *Cylindrotoma splendens.* The species of Tipula and other genera the females of which have blunt valves to the ovipositor (Styringomyia, Macromastix, and others), all probably scatter their eggs promiscuously or else have a specialized method of egg-laying. Similarly, the species of Tipula of the *arctica* group, in which the dorsal valves of the ovipositor are very large, placed horizontally, and with the margin finely serrated, undoubtedly have a peculiar method of oviposition, but this has not yet been observed.

The egg

The number of eggs laid by crane-flies varies from about forty-five in Styringomyia to some two thousand in the larger species of Eriocera. The following table indicates the general range in the group:

Species	Number of eggs laid			Reference
	Maximum	Minimum	Average	
Ptychoptera albimana	587	520	554	Topsent, 1914–16
Styringomyia didyma	45	....	45	Terry ms.
Eriocera longicornis	1,034	872	952	Alexander ms.
spinosa	2,061	1,824	1,942	Alexander ms.
Hexatoma megacera	372	316	347	Alexander, 1915 c
Phalacrocera replicata	60	....	60	Miall and Shelford, 1897
Liogma glabrata	60	....	60	Müggenberg, 1901
Ctenophora angustipennis	400	200	300	Lovett, 1915
Tipula cunctans	....	....	300	Hyslop, 1910
bicornis	297	282	289	Webster, 1893 b
tephrocephala	255	....	255	Webster, 1893 b
angustipennis	602	....	602	Hyslop, 1910
collaris	329	....	329	Alexander ms.
dejecta	366	251	309	Alexander ms.
oleracea	600	....	600	Del Guercio, 1914

The eggs are in most cases elongate with the ends narrowed and rounded, or, in other words, spindle-shaped. The chorion in the species of Tipula, Hexatoma, and other genera is blackened and in some cases more or less sculptured. In *Ctenophora angustipennis* (Lovett, 1915) the egg is ebony black with deep purple reflection, elongate-oval, uniform, without pits or ridges, and measuring from 1.26 to 1.4 millimeters by 0.375 millimeter.

In *Tipula bicornis* (Webster, 1893 b) the egg is 0.8 millimeter long by 0.3 to 0.4 millimeter in diameter, elongate-ovoid, with one side deeply concave, the surface highly polished. The egg of *Nephrotoma ferruginea* is smaller, with five distinct grooves. The egg of *Tipula glacialis* (Pokorny, 1887:53) is described as being 1.2 millimeters long and only 0.3 millimeter in diameter, cylindrical, the two ends equally rounded, the surface smooth, shiny black, with faint steel-blue or purplish red reflections. In many other genera of Tipulidae, especially the smaller forms, the eggs are soft and whitish or nearly hyaline. In a few species the eggs take on a decided green or greenish tinge. The egg of *Cylindrotoma splendens* is described elsewhere in this paper (page 709). The egg of *Ptychoptera albimana*, as described by Topsent (1914–16), measures 0.825 by 0.264 millimeter, and is pale yellow, slightly arcuated, and with the surface curiously ornamented.

The larva

As a rule, the larvae live in the haunts where the eggs are laid. The duration of the larval stage varies from about a month in Styringomyia (larva and pupa together, thirty-seven days — Terry ms.) to the greater part of a year in most crane-flies. Many of the smaller species of Erioptera, Ormosia, Rhaphidolabis, and other genera are on the wing in the spring and again in the fall, and with little doubt are double-brooded. This would make the larval existence but a few months, but still probably longer than the other stages taken together. This problem of double broods should be worked out carefully. It often appears that there are two broods, when in reality there may be two developing generations, each passing the winter as larvae, but one attaining its growth much more slowly in the spring and summer and not maturing until late summer. Phalacrocera and *Cylindrotoma splendens* spend about eleven months in the larval stage (Bengtsson 1897, and Cameron 1918), while *Tipula paludosa* spends nine months in that stage (Rennie, 1917). It is probable that nearly all crane-flies in the North Temperate Zone winter normally as larvae. The growth during summer, fall, and winter is very slight, but in the spring it is greatly accelerated and in a month the larva may attain its full growth. Larvae of *Tipula ignobilis* taken at Ithaca, New York, on April 23, 1917, measured only 6.5 millimeters in length; on May 19 they had attained their full growth of 18 millimeters and were ready to pupate. *Cylindrotoma splendens* spends the winter as a larva,

9 millimeters in length, but grows rapidly during the spring, attaining its full size (17 millimeters) in two months of growth. *Liogma glabrata* spends the winter as a very small larva, but in the spring its growth is greatly accelerated.

The haunts in which the larvae of crane-flies occur are exceedingly varied. In the case of single large genera, such as Dicranomyia and Tipula, the species range from those that are almost strictly aquatic to others that are entirely terrestrial, living in decaying wood or even mining in the leaves of plants.

The transition between strictly aquatic and terrestrial forms is very gradual, as was pointed out by Miall (1895:11) some years ago when he wrote:

> How did insects ever come to seek the water, seeing that their mode of respiration is primarily adapted to another element? We can see almost all the steps of the adaptation on the shores of our rivers, lakes and seas. We can see dipterous larvae which, like the " leather jacket " (the larva of the daddy-long-legs), burrow in the ground for their vegetable food, and devour the roots of grasses. Other larvae of the same family (Tipulidae) prefer moist earth in the neighborhood of streams. Others again live immersed in water, or mud saturated with water, though they come to the surface at times and push their tails, which carry the spiracles, into the air. Some few have become so completely aquatic that they seldom, if ever, come to the surface, and all their supply of oxygen is obtained from the water.

The culmination of this latter condition is reached in forms such as Antocha and related genera and species. Crampton (1919:100) has made similar observations on the subject.

The haunts of the larvae of crane-flies are best shown by the following table, in which the various species are arranged according to habitat, from the strictly aquatic to the various terrestrial forms:

Habitat	Species
Strictly aquatic, in silken cases	Antocha
In very rapid water (lotic) on or in submerged mosses (hygropetric association)	*Dicranomyia simulans*, Pedicia, Triogma, Tipuline No. 1, and others
Aquatic, on submerged plants	Phalacrocera, Triogma
Semi-aquatic (part of life spent in water, but pupation taking place on land)	*Dicranomyia simulans*, Eriocera, Hexatoma, Aeshnasoma, Longurio, *Tipula abdominalis*, *T. caloptera*, *T. bella*, and others
On cliffs and wooden walls, usually in silken cases covered by water	*Dicranomyia simulans*, Geranomyia, Elliptera, Dactylolabis, and others
In cold springs	Pedicia, Thaumastoptera

Habitat	Species
In stagnant water in the axils of bromeliaceous and other plants	Trentepohlia, *Gnophomyia rufa*
Amphibious in decaying wood	Protoplasa (supposition), Epiphragma
In mud or sand:	
a. In open swamps	Bittacomorpha, Ptychoptera, Rhamphidia, *Erioptera septemtrionis*, *E. chlorophylla*, *E. vespertina*, *Limnophila adusta*, *L. macrocera*, *Pilaria recondita*, *P. tenuipes*, *P. quadrata*, *Tricyphona inconstans*, Prionocera, *Tipula dejecta*, *T. sayi*, *T. tricolor*, and others
b. In shaded woods	Bittacomorphella, *Ormosia innocens*, *Erioptera megophthalma*, *Molophilus hirtipennis*, Ulomorpha, Dicranophragma, Penthoptera, *Tipula cayuga*, and others
c. Along the margins of streams and other bodies of water	*Limnobia fallax*, *Erioptera* (*Hoplolabis*) *armata*, Trimicra, *Gonomyia* (*Leiponeura*) *alexanderi*, *G. kansensis*, Eriocera, Hexatoma, and others
In or beneath damp cushions of moss	*Dicranomyia badia*, *D. stulta*, *Tipula oropezoides*, *T. collaris*, *T. nobilis*, *T. ignobilis*, and others
In or beneath dry cushions of moss	Liogma, Dolichopeza, Oropeza, and others
In dry soil	Dicranoptycha, Cladura, *Nephrotoma ferruginea*, *Tipula cunctans*, *T. angustipennis*, and others
In fungi	*Limnobia triocellata*, *L. cinctipes*, Ula, and others
In decaying vegetables, plant stems, manure, and like situations	Trichocera, *Limnobia indigena*, *Rhipidia domestica*, *R. maculata*, and others
In wood:	
a. In decaying wood, usually just beneath the bark	*Dicranomyia rara*, *D. macateei*, *Rhipidia fidelis*, *R. bryanti*, Elephantomyia, Teucholabis, Gnophomyia, *Limnophila unica*, Brachypremna, Ctenophora, Dictenidia, *Tipula trivittata*, *T. usitata*, and others
b. In nearly solid wood	Tanyptera
On leaves of terrestrial plants:	
a. On flowering plants	Cylindrotoma
b. On mosses	Liogma, Triogma (in some instances)
Mining in the leaves of plants	*Dicranomyia foliocuniculator*

Feeding.— The various larvae of crane-flies show a considerable diversity in their habits of feeding. The majority of species, as known, are herbivorous, but a large group are decidedly carnivorous in their habits.

The Tipulinae feed on the living vegetable tissue or plant remains occurring in their habitat, or, when pressed for food, they will eat earth-

worms (Patterson, 1908) and other soft-bodied animals. Dissections of *Tipula abdominalis* show the food of this species to consist principally of small filamentous algae, diatoms (Diatoma, Navicula, and others), and rootlets of small plants. The alimentary tract is often crammed with sand or soil particles. The species of Tipula and Nephrotoma that are injurious to plants, considered later in this paper under the heading *Economic Importance*, effect their damage by devouring the living tissues of the roots. The Cylindrotominae feed on the living tissues of the plants on which they dwell; in the case of Phalacrocera, Triogma, and Liogma these are mosses, in Cylindrotoma they are the parenchyma and epidermis of higher plants (spermatophytes). With this habit of feeding on plant tissues the extreme of sluggishness of motion is attained. The wood-boring species of Tipulinae (such as the species of Tanyptera and Ctenophora) feed on the ligneous tissue of the trees in which they occur. Other species of crane-flies injure young seedlings by destroying the bark and the bast tissues.

The hexatomine and pediciine forms represent the opposite extreme, being for the most part carnivorous or even cannibalistic in their habits. In order to capture their prey they are of necessity rapid of movement, and in this group the most graceful and active of all tipulid larvae are found. The motions of the species are, at times, exceedingly agile and snakelike. The food consists of a variety of animal forms. Dicranota has been recorded as feeding on worms of the genus Tubifex. Pedicia usually feeds on the larvae of small insects, especially Chironomidae, but the large species of this genus and of Eriocera are capable of capturing almost any insect of a size equal to their own. The larvae of *Eriocera spinosa* are able to inflict painful bites on tender parts of the skin of a man. Penthoptera, Eriocera, Hexatoma, and most of the limnophiline groups likewise feed largely on midge larvae. From one small larva of *Limnophila* (*Dicranophragma*) *fuscovaria* the writer has dissected out the remains of two large midge larvae, whose heads were nearly half the size of that of the captor. The chitinized mentum in these predacious forms is very weak or is lacking, allowing for a tremendous distension of the gular region. The mandibles are always developed into powerful curved hooks which serve well their purpose of grasping and holding the victims. The esophageal region is often retrorsely roughened to prevent the egress of anything that has once started down the throat. In addition to the

various chitinized jaws, legs, heads, and other insect remains, the distended proventricular regions usually show a considerable amount of sand particles and much plant tissue.

The pupa

When ready to pupate, the larva ceases feeding and becomes much contracted and sluggish. The pupa is formed within the last larval skin, which is then shed completely except in certain Cylindrotominae and a few scattered genera in other tribes, in which cases the larval skin adheres to the posterior end of the abdomen. The pupal existence is spent in or near the haunts of the larva.

In the strictly aquatic genus Antocha the pupa lives in water in a silken case, respiration being accomplished by means of the many-branched breathing horns. The species of Elliptera and certain Dicranomyia (*simulans*, for example) approach this aquatic condition. The other species of crane-flies with aquatic larvae known to the writer go to the soil in order to pupate, this category including Eriocera, Hexatoma, *Tipula caloptera*, *T. abdominalis*, and many others.

The pupae of some, at least, of the Cylindrotominae attach themselves to plant stems for the purpose of pupation. The leaf-mining *Dicranomyia foliocuniculator* pupates within the larval passages. The majority of the limnobiine forms spend the pupal existence in silken cases to which pebbles and particles of débris or plant tissues adhere.

The pupae of the Ptychopteridae have one of the two breathing horns enormously elongated, the tip of this being projected above the water level into the air for respiration. Certain tipuline crane-flies have a somewhat similar development of the breathing horns, discussed later.

The duration of the pupal existence is remarkably uniform thruout the group, averaging from six to eight days. The following table illustrates this for the more representative genera and species. Records which have not been determined sufficiently close, and which as stated are probably too long, are indicated by an asterisk.

Species	Duration of pupal existence (days)			Reference
	Maximum	Minimum	Average	
Ptychoptera rufocincta	....	$4\frac{3}{4}$	....	Alexander ms.
albimana	*12	10	11	Topsent, 1914–16
Bittacomorphella	*13	....	....	Alexander ms.
Dicranomyia badia	7	....	7	Alexander ms.
stulta	*8	....	....	Alexander ms.
Rhipidia bryanti	7	....	7	Shannon ms.
Limnobia cinctipes	....	5	....	Alexander ms.
triocellata	9	8	$8\frac{1}{2}$	Alexander ms.
Rhamphidia mainensis	6	....	6	Alexander ms.
Dicranoptycha winnemana	*10	....	....	Alexander ms.
Ula elegans	*10	....	....	Alexander, 1915a
Epiphragma	....	6	6	Alexander ms.
Pseudolimnophila	9	8	$8\frac{1}{2}$	Alexander ms.
Limnophila macrocera	9	8	$8\frac{1}{2}$	Alexander ms.
fuscovaria	*14	8	10	Alexander ms.
Pilaria	7	7	7	Alexander ms.
Ulomorpha	*9	....	....	Alexander ms.
Eriocera fultonensis	7	7	7	Alexander ms.
longicornis	7.3	....	7.3	Alexander ms.
Hexatoma megacera	$6\frac{1}{2}$	....	$6\frac{1}{2}$	Alexander ms.
Pedicia rivosa	*14	7	$10\frac{1}{2}$	Beling, 1879:46
Erioptera macrophthalma	8	7	$7\frac{1}{2}$	Alexander ms.
Molophilus hirtipennis	*10	....	....	Alexander ms.
Gnophomyia tristissima	5	4	$4\frac{1}{2}$	Hyslop ms.
Ormosia nigripila	*11	....	....	Alexander ms.
Teucholabis complexa	9	....	......	Johnson ms.
Elephantomyia	8	6	7	Shannon ms.
Cylindrotoma splendens	10	6	8	Cameron, 1918
Liogma glabrata	11	10	$10\frac{1}{2}$	Müggenberg, 1901
Phalacrocera replicata	8	7	$7\frac{1}{2}$	Bengtsson, 1897
Dolichopeza albipes	6	....	6	Beling, 1886 (as *sylvicola*
Ctenophora angustipennis	....	....	10	Lovett, 1915
Dictenidia bimaculata	7	....	7	Beling, 1873b
Tipula maxima	*14	*10	*12	Beling, 1886
oleracea	8	7	$7\frac{1}{2}$	Del Guercio, 1914:315
cayuga	7.6	....	7.6	Alexander ms.
ignobilis	8	7	$7\frac{1}{2}$	Alexander ms.
dejecta	8	....	8	Alexander ms.
collaris	8	7	$7\frac{1}{2}$	Alexander ms.
Nephrotoma lineata	7	....	7	Beling, 1879 (as *histrio*)
lunulicornis	7	....	7	Beling, 1879
analis	*12	*8	*10	Beling, 1886

ENEMIES

Crane-flies have many enemies and but few means of combating them. Every stage of the crane-fly's existence is fraught with danger. The larvae of the majority of species are soft-bodied, herbivorous creatures, which form a choice morsel of food for carnivorous forms of many classes and orders. The period when the adult fly has just emerged from the pupal hull is undoubtedly the one in which the greatest danger is found, for then the insects are teneral and incapable of rapid motion. The adult flies are sometimes drowned in the sea or other large bodies of water and their dead fragments cast up in windrows on the shore. A very unusual instance of this kind is recorded for *Tipula oleracea* by Patterson (1908). At their best, the adult flies are poor, awkward fliers and are easily captured by a wide range of species, as indicated in the following pages.

Predatory natural enemies

Vertebrates

Mammalia.— Undoubtedly many of the smaller mammals prey on the larvae of various species of Tipula. In another paper (Alexander, 1919 d: 776–777) the writer has discussed the value of the larvae of an undetermined species of Tipula in the Pribilof Islands as an article of food for the arctic fox. These larvae occur in enormous numbers beneath the lichens of the tundra and the foxes can easily get them at a time when other food is scarce or unobtainable. Mice, shrews, and moles find an important element of their food from this source. White (1914) states that in North Wales the European mole, *Talpa europaea,* eats, on an average, twenty crane-fly larvae a day, these constituting one of the main foods of this mammal.

Aves.— Birds are well-known enemies of crane-flies, both in their immature stages and as adult flies. Hyslop (1910:129–130) lists ninety-one species of birds which are known to feed on crane-flies. Baer (1913) describes ravens and starlings as feeding on the larvae of a species of Tipula. While working with the United States Biological Survey, the writer was given the opportunity to examine files for records. His thanks for assistance in this work are due to Messrs. Kalmbach, McAtee, and Wetmore. The records of the Survey are based on an examination of the contents of the stomachs of many thousands of individuals, and furnish very valuable and fairly complete data on the North American

birds which prey on various stages of the Tipulidae. These records are here arranged according to the latest check list of the American Ornithologists' Union:[3]

Longipennes:
  Laridae:
    Larus delawarensis Ord. Ring-billed gull
    L. franklinii Rich. Franklin's gull
    Sterna hirundo Linn. Common tern
Anseres:
  Anatidae:
    Mergus americanus Cass. Merganser
    Anas platyrhynchos Linn. Mallard
    A. rubripes Brewst. Black duck
    Mareca americana (Gmel.). Baldpate
    Nettion carolinense (Gmel.). Green-winged teal
    Dafila acuta (Linn.). Pintail
    Aix sponsa (Linn.). Wood duck
Herodiones:
  Ardeidae:
    Egretta candidissima candidissima (Gmel.). Snowy egret
    Butorides virescens virescens (Linn.). Green heron
Limicolae:
  Phalaropodidae:
    Phalaropus fulicarius (Linn.). Red phalarope
    Lobipes lobatus (Linn.). Northern phalarope
    Steganopus tricolor Vieill. Wilson's phalarope
  Recurvirostridae:
    Recurvirostra americana Gmel. Avocet
    Himantopus mexicanus (Müll.). Black-necked stilt
  Scolopacidae:
    Philohela minor (Gmel.). American woodcock
    Gallinago delicata (Ord). Wilson's snipe
    Arquatella maritima maritima (Brünn.). Purple sandpiper
    Pisobia aurita (Lath.). Sharp-tailed sandpiper
    P. maculata (Vieill.). Pectoral sandpiper
    P. bairdii (Coues). Baird's sandpiper
    Limosa fedoa (Linn.). Marbled godwit
    Totanus flavipes (Gmel.). Yellow-legs
    Heteractitis incanus (Gmel.). Wandering tatler
    Bartramia longicauda (Bechst.). Bartramian sandpiper
  Charadriidae:
    Charadrius dominicus dominicus (Müll.). Golden plover
    Oxyechus vociferus (Linn.). Killdeer
  Aphrizidae:
    Arenaria interpres interpres (Linn.). Turnstone
Gallinae:
  Tetraonidae:
    Bonasa umbellus umbellus (Linn.). Ruffed grouse
Raptores:
  Buteonidae:
    Ictinia mississippiensis (Wils.). Mississippi kite

[3] Check list of North American birds, 3d ed., p. 1–430. American Ornithologists' Union. 1910.

Coccyges:
  Cuculidae:
    Coccyzus americanus americanus (Linn.). Yellow-billed cuckoo
    C. erythrophthalmus (Wils.). Black-billed cuckoo
    Cuculus canorus telephonus Heine. Kamchatka cuckoo
Pici:
  Picidae:
    Dryobates pubescens pubescens (Linn.). Downy woodpecker
    D. nuttallii (Gamb.). Nuttall's woodpecker
    Sphyrapicus varius varius (Linn.). Yellow-bellied sapsucker
    S. thyroideus (Cass.). Williamson's sapsucker
    Melanerpes erythrocephalus (Linn.). Red-headed woodpecker
    Asyndesmus lewisi Riley. Lewis's woodpecker
    Colaptes auratus auratus (Linn.). Flicker
Macrochires:
  Caprimulgidae:
    Antrostomus carolinensis (Gmel.). Chuck-will's-widow
    Chordeiles virginianus virginianus (Gmel.). Nighthawk
    C. acutipennis texensis Lawr. Texas nighthawk
  Cypselidae:
    Chaetura pelagica (Linn.). Chimney swift
    C. vauxi (J. K. Towns.). Vaux's swift
    Aëronautes melanoleucus (Baird). White-throated swift
  Trochilidae:
    Calypte anna (Less.). Anna's humming bird
    Selasphorus rufus (Gmel.). Rufous humming bird
Passeres:
  Tyrannidae:
    Tyrannus tyrannus (Linn.). Kingbird
    T. verticalis Say. Arkansas kingbird
    T. vociferans Swains. Cassin's kingbird
    Myiarchus crinitus (Linn.). Great-crested flycatcher
    Sayornis phoebe (Lath.). Phoebe
    S. sayus (Bonap.). Say's phoebe
    S. nigricans (Swains.). Black phoebe
    Myiochanes virens (Linn.). Wood pewee
    M. richardsonii richardsonii (Swains.). Western wood pewee
    Empidonax flaviventris (W. M. & S. F. Baird). Yellow-bellied flycatcher
    E. difficilis difficilis Baird. Western flycatcher
    E. virescens (Vieill.). Acadian flycatcher
    E. traillii traillii (Aud.). Traill's flycatcher
    E. minimus (W. M. & S. F. Baird). Least flycatcher
    E. wrightii Baird. Wright's flycatcher
    E. griseus Brewst. Gray flycatcher
  Corvidae:
    Pica pica hudsonia (Sab.). American magpie
    Cyanocitta cristata cristata (Linn.). Blue jay
    C. stelleri stelleri (Gmel.). Steller's jay
    Corvus brachyrhynchos brachyrhynchos Brehm. American crow
    C. ossifragus Wils. Fish crow
  Sturnidae:
    Sturnus vulgaris Linn. Starling
  Icteridae:
    Dolichonyx oryzivorus (Linn.). Bobolink
    Molothrus ater ater (Bodd.). Cowbird

Passeres (*continued*):
  Icteridae (*continued*):
    Xanthocephalus xanthocephalus (Bonap.). Yellow-headed blackbird
    Agelaius phoeniceus phoeniceus (Linn.). Red-winged blackbird
    A. gubernator californicus Nels. Bicolored redwing
    Sturnella magna magna (Linn.). Meadow lark
    Icterus spurius (Linn.). Orchard oriole
    I. galbula (Linn.). Baltimore oriole
    I. bullockii (Swains.). Bullock's oriole
    Euphagus cyanocephalus (Wagl.). Brewer's blackbird
    Quiscalus quiscula quiscula (Linn.). Purple grackle
  Fringillidae:
    Leucosticte griseonucha (Brandt). Aleutian rosy finch
    Plectrophenax nivalis nivalis (Linn.). Snow bunting
    P. hyperboreus Ridgw. McKay's snow bunting
    Calcarius lapponicus lapponicus (Linn.). Lapland longspur
    Passerculus sandwichensis savanna (Wils.). Savanna sparrow
    Zonotrichia leucophrys leucophrys (J. R. Forst.). White-crowned sparrow
    Z. albicollis (Gmel.). White-throated sparrow
    Junco hyemalis hyemalis (Linn.). Slate-colored junco
    Passer domesticus (Linn.). English sparrow
    Melospiza melodia melodia (Wils.). Song sparrow
    M. lincolnii lincolnii (Aud.). Lincoln's sparrow
    M. georgiana (Lath.). Swamp sparrow
    Passerella iliaca iliaca (Merr.). Fox sparrow
    Pipilo erythrophthalmus erythrophthalmus (Linn.). Towhee
    Passerina amoena (Say). Lazuli bunting
  Tangaridae:
    Piranga ludoviciana (Wils.). Western tanager
    P. erythromelas (Vieill.). Scarlet tanager
    P. rubra rubra (Linn.). Summer tanager
  Hirundinidae:
    Progne subis subis (Linn.). Purple martin
    Petrochelidon lunifrons lunifrons (Say). Cliff swallow
    Hirundo erythrogastra Bodd. Barn swallow
    Iridoprocne bicolor (Vieill.). Tree swallow
    Tachycineta thalassina lepida Mearns. Northern violet-green swallow
    Riparia riparia (Linn.). Bank swallow
    Stelgidopteryx serripennis (Aud.). Rough-winged swallow
  Bombycillidae:
    Bombycilla cedrorum Vieill. Cedar waxwing
  Vireonidae:
    Vireosylva olivacea (Linn.). Red-eyed vireo
    V. philadelphica (Cass.). Philadelphia vireo
    V. gilva gilva (Vieill.). Warbling vireo
    Lanivireo solitarius solitarius (Wils.). Blue-headed vireo
    Vireo griseus griseus (Bodd.). White-eyed vireo
    V. bellii bellii Aud. Bell's vireo
    V. bellii pusillus Coues. Least vireo
  Mniotiltidae:
    Mniotilta varia (Linn.). Black-and-white warbler
    Helmitheros vermivorus (Gmel.). Worm-eating warbler
    Dendroica aestiva aestiva (Gmel.). Yellow warbler
    D. coronata (Linn.). Myrtle warbler
    D. auduboni auduboni (Towns.). Audubon's warbler

Passeres (*continued*):
- Mniotiltidae (*continued*):
  - *D. dominica dominica* (Linn.). Yellow-throated warbler
  - *Oporornis tolmiei* (J. K. Towns.). Macgillivray's warbler
  - *Geothlypis trichas trichas* (Linn.). Maryland yellowthroat
  - *Icteria virens virens* (Linn.). Yellow-breasted chat
  - *Wilsonia pusilla pusilla* (Wils.). Wilson's warbler
  - *Setophaga ruticilla* (Linn.). American redstart
- Motacillidae:
  - *Anthus rubescens* (Tunst.). Pipit
- Mimidae:
  - *Mimus polyglottos polyglottos* (Linn.). Mocking bird
  - *Dumetella carolinensis* (Linn.). Catbird
  - *Toxostoma rufum* (Linn.). Brown thrasher
  - *T. redivivum* (Gamb.). Californian thrasher
- Troglodytidae:
  - *Heleodytes brunneicapillus couesi* (Sharpe). Cactus wren
  - *Salpinctes obsoletus obsoletus* (Say). Rock wren
  - *Catherpes mexicanus punctulatus* Ridgw. Dotted canon wren
  - *Thryothorus ludovicianus ludovicianus* (Lath.). Carolina wren
  - *Thryomanes bewickii bewickii* (Aud.). Bewick's wren
  - *Nannus hiemalis hiemalis* (Vieill.). Winter wren
  - *Telmatodytes palustris palustris* (Wils.). Long-billed marsh wren
- Paridae:
  - *Baeolophus inornatus inornatus* (Gamb.). Plain titmouse
  - *Penthestes atricapillus atricapillus* (Linn.). Chickadee
  - *P. carolinensis carolinensis* (Aud.). Carolina chickadee
  - *P. gambeli gambeli* (Ridgw.). Mountain chickadee
  - *P. hudsonicus hudsonicus* (Forst.). Hudsonian chickadee
  - *Psaltriparus minimus minimus* (J. K. Towns.). Bush-tit
- Chamaeidae:
  - *Chamaea fasciata fasciata* (Gamb.). Wren-tit
- Sylviidae:
  - *Regulus calendula calendula* (Linn.). Ruby-crowned kinglet
- Turdidae:
  - *Myadestes townsendi* (Aud.). Townsend's solitaire
  - *Hylocichla mustelina* (Gmel.). Wood thrush
  - *H. fuscescens fuscescens* (Steph.). Veery
  - *H. aliciae aliciae* (Baird). Gray-cheeked thrush
  - *H. ustulata ustulata* (Nutt.). Russet-backed thrush
  - *H. ustulata swainsoni* (Tschudi). Olive-backed thrush
  - *H. guttata pallasii* (Cab.). Hermit thrush
  - *Planesticus migratorius migratorius* (Linn.). American robin

The principal families that feed on the adult flies are the Caprimulgidae, the Cypselidae, the Tyrannidae, the Icteridae, the Hirundinidae, the Mniotiltidae, the Troglodytidae, the Paridae, and the Turdidae.

Many species of birds feed on the larvae of crane-flies, the more notable of these being the water-fowl, Anatidae, the shore birds, Scolopacidae, and the thrushes, Turdidae. Sim (1907) has recorded the chestnut-sided warbler, *Dendroica pensylvanica* (Linn.) as feeding on *Tipula* sp.

In Europe the raven and the starling are important, as already stated. Patterson (1908) records the starling as eating great numbers of *Tipula oleracea* and as boring into the soil in search of the larvae of this species.

It will be noted that in the foregoing list no species of doves or pigeons are recorded in this country as feeding on Tipulidae. The following note on an Australian pigeon shows the importance of the larvae as a food for these birds: [4]

Mr. North exhibited the head, crop, and gizzard of a wonga-wonga pigeon (*Leucosarcia picata* Lath.) shot by Mr. H. J. McCooey in a myrtle scrub at Upper Burragorang on the 21st inst. The crop is absolutely crammed with dipterous larvae (*Habromastix cinerascens* Sk.) and undigested portions of them mixed with seeds, berries, and earth appear also in the gizzard. As the larvae are known to be destructive to grass, the wonga-wonga would appear to be deserving of consideration.

Amphibia.— Crane-flies, both larvae and adults, form a considerable element of the food of many Amphibia. The studies by Needham (1905:13) show this to be true in the case of the bullfrog, *Rana catesbeiana* Shaw. Munz (1920) studied the food habits of eight species of Anura and found that five fed on crane-fly larvae or adults. These species were *Rana clamitans* Latr., *R. sylvatica* Lec., *R. palustris* Lec., *R. pipiens* Schreb., and *Hyla crucifer* Wied. The following additional records are given:

Desmognathus fusca Raf. Dusky salamander. Wings of a Limnophila found in a specimen from Ithaca, New York. (A. A. Noyes.)

Rana clamitans Latr. Green frog. Two larvae of a Tipula, near *dejecta* Walker, found in stomach. (S. W. Frost.)

Bufo lentiginosus woodhousei Girard. Centerville, Utah, April 27, 1912. Twenty-six per cent of the food of this species consisted of a large tipulid. (E. R. Kalmbach.)

Bufo sp. Washington, D. C., May 17, 1890. One per cent tipulid larvae. (W. L. McAtee.)

Pisces.— The larvae of crane-flies furnish favorite morsels for many carnivorous species of fish, and as a consequence they are in considerable demand with fishermen as bait for bass and other game fish. These include the larvae of the larger species of Eriocera and many large semiaquatic species of Tipula, especially *Tipula caloptera* and *T. abdominalis*. Fragments of the adult flies are often found in the stomach contents of fish, notably species of trout, most of these pieces being of individuals that

[4] Linn. Soc. New South Wales. Proc., ser. 2:9:585. 1894.

had fallen into the water or were captured while newly transformed. Forbes (1888) records Coregonus and Hyodon as feeding on the eggs, and Notropis as feeding on the larvae, of crane-flies. Levander (1909:1) records *Perca fluviatilis* Linn. as feeding on larvae of Tipulidae.

Invertebrates

Arachnida.— Some spiders are notable enemies of crane-flies, which fall easy victims while in a helpless, teneral condition. These spiders represent many families, such as the Thomisidae, the Lycosidae, the Attidae, the Epeiridae, and others (Alexander and Lloyd, 1914:15; also, Alexander, 1915 c:144). An account of their preying on the larger crane-flies of the genus Tipula is given under the discussion of *T. taughannock* (page 1013). In a recent paper Bilsing (1920) has recorded four species of crane-flies eaten by spiders. These spiders represented thirteen species arranged in four families — the Lycosidae, the Attidae, the Epeiridae, and the Agelenidae. J. R. Malloch found a female *Tipula angustipennis* which was being eaten by a crab spider, determined by Mr. Banks as *Xysticus ferox* Htz. The spider did not release its hold until after it was placed in a jar of cyanide.

Hexapoda.— Odonata: The following records of dragon-flies found feeding on adult crane-flies are available: *Gomphus vastus* Walsh and *G. ventricosus* Walsh, found feeding on *Tipula bicornis* at South Bend, Indiana, May 30, 1914 (E. B. Williamson); *Helocordulia uhleri* (Selys), found feeding on *Eriocera longicornis* (Alexander, 1915 c:152); *Agrion puella* Linn., found feeding on *Erioptera flavescens* (Campion, 1914:498). C. H. Kennedy has sent the writer a male and a female specimen of a small crane-fly, *Teucholabis pabulatoria* Alex., which he found in the mouth of a damsel fly, *Hetaerina tricolor* Burm., collected in Guatemala by Professor Hine. Needham and Hart (1901–03 [1901]:47) record the nymphs of *Anax junius* (Dru.) feeding on the larvae of Tipulidae.

Diptera: The adult flies of at least three families of the order Diptera — the Asilidae, the Empididae, and the Scatophagidae — and the larvae of a fourth, Anthomyiidae, are notable enemies of crane-flies. The records of Kirby (1892), Poulton (1906–07), Bromley (1914), Alexander (1915 c), and McAtee and Banks (1920) on the first three of these families may be summarized as follows:

Asilidae (robber flies)	Prey
Lasiopogon cinctus (Fabr.)	*Nephrotoma lineata* (Scop.) (Poulton, 1906–07, as *histrio* [Fabr.])
Neoitamus cyanurus (Lw.) (in copulation with female, the latter with the crane-fly)	*Tipula scripta* Meig. (Poulton, 1906–07)
Proctacanthus philadelphicus Macq.	*Nephrotoma* sp. (2 records, Bromley, 1914)
Asilus sp.	*Nephrotoma ferruginea* (Fabr.) (3 records, Alexander, 1915 c)
Asilus flavofemoratus Hine	*Tipula* sp. (McAtee and Banks, 1920: 30)
Asilus notatus Wied.	*Nephrotoma ferruginea* (Fabr.) (McAtee and Banks, 1920: 31)
Asilus paropus Walk.	*Epiphragma solatrix* (O. S.) (McAtee and Banks, 1920: 31)
Asilinae	*Tipula lateralis* Meig. (Poulton, 1906–07)

The Empididae, or dance flies, are small, predacious flies which are closely related to the robber flies and largely replace them in moist shaded situations. They unquestionably play a most important part in the economy of the Tipulidae, since both groups are practically confined to the same general situations and, in the temperate regions at least, representatives of the two groups are invariably found together. Macquart (Kirby, 1892: 229), discussing *Empis livida* Linn., writes as follows: "Among the thousands of pairs which I have noticed resting on bushes or hedges, nearly all the females were engaged in sucking some insect, sometimes small Phryganidae or Ephemeridae, but more often Tipulidae. They busy themselves with feeding and perpetuating their species at the same time." Howlett (1907) records *Empis borealis* Linn. as feeding on Tipulidae. The following records are from Poulton (1906–07: 380–382): *Empis tesselata* Fabr. preys on *Tipula lunata* Linn., *T. paludosa* Meig., and other species; *Empis livida* Linn. preys on *Dicranomyia* sp. (It is probable that the long-legged flies, Dolichopodidae, likewise play an important rôle in the lives of the Tipulidae, but no records are available to the writer to confirm this belief.)

The Scatophagidae (Cordyluridae), or dung flies, unquestionably play an important part in the lives of the smaller crane-flies (Limnobiinae). The following records indicate this relationship, the last being supplied by Malloch:

Enemy	Prey
Scatophaga suilla (Fabr.)	*Dicranomyia lutea* (Meig.) (Poulton, 1906–07)
Scatophaga sp. (*stercoraria?*)	*Erioptera* sp. (Poulton, 1906–07)
Scatophaga sp.	*Hexatoma megacera* (O. S.) (Alexander, 1915 c)
Scatophaga stercoraria (L.) and *squalida* Meig.	*Trichocera* (Malloch, 1911)

Comparatively recently the larvae of Anthomyiidae have been found to play a highly important rôle in the economy of other insects living in the same haunts. The very important paper by Keilin (1917) may be consulted in connection with this point. This student found the following Anthomyiidae associated with Tipulidae: *Graphomyia maculata* Scop., feeding on larvae of *Ptychoptera contaminata* (L.) (Keilin, 1917: 354–360); *Allognota agromyzina* Fall., associated with and possibly feeding on the larvae of *Ula macroptera* Macq. (page 360–362 of reference cited); *Phaonia cincta* Zett., feeding on larvae and pupae of *Mycetobia pallipes* (page 362–375 of reference); *Phaonia goberti* Mik, associated with and possibly feeding on the larvae of *Gnophomyia tripudians* Bergr. (page

375–377 of reference); *Mydaea pertusa* Meig., possibly feeding on larvae of Tipulidae (page 393–396 of reference).

A species of Phaonia with presumably parasitic habits is discussed on page 732 of this memoir.

Coleoptera: The adults and the larvae of the following species of ground beetles (Carabidae) have been recorded as important enemies of crane-flies (Hyslop, 1910): *Poecilus lucublandus* Say; *Micromaseus femoralis* (Kirby); *Platynus* sp.; *Harpalus pennsylvanicus* Dej.; *H. caliginosus* Fabr. Most of these were recorded by Webster (1893 a:241) as feeding on the injurious crane-fly *Tipula bicornis*.

The larvae of Elateridae (wireworms) are enemies of crane-flies. The writer has seen several feeding on large larvae of *Tipula trivittata*.

Hymenoptera: Ants (Formicidae) undoubtedly capture and devour many crane-flies, these generally being pupae or teneral adults. Hyslop (1910) cites the record of an *Aphaenogaster fulva* Roger which was observed dragging a living adult tipulid over the ground. Chapman (1918:191) records feeding species of Myrmica on adult Tipulidae which were readily eaten by the ants in preference to most other insect food. On August 2, 1917, at Larned, Pawnee County, Kansas, along the bank of the Arkansas River, the writer noted a small ant which was dragging a still living pupa of *Gonomyia kansensis* from its burrow in the sand at the bank of the river. The ant had the pupa about the head and carried it off despite its struggles. Both the Gonomyia and the formicid were common and the tragedy as described was not accidental.

The Pemphredonidae (Mimesinae) and the Crabronidae, fossorial wasps in the Hawaiian Islands, bear an important relationship to the smaller Tipulidae dwelling in the same haunts. Writing of the Mimesinae, a subfamily of the Pemphredonidae, Perkins (1913:lxxxv) says:

All the Hawaiian species of both genera are true forest insects and most of them may be seen in large numbers, where they occur, flying around ferns and bushes in sunny places. The males are often much more numerous apparently than the females, but this is due to the more retiring habits of the latter, which, when they have begun to provision their nests, frequent dark, shady and damp places in search of their prey. This consists of the endemic Limnobiidae or daddy longlegs, which live in such places. . . . Although I have often watched females of these wasps returning with prey to their burrows, it was always Tipulidae that they carried to the nest. Their burrows are usually made in the ground and are often drilled down from beneath a stone, this no doubt serving to keep the burrow sufficiently dry.

Referring to Limnobiinae, Perkins says (page clxxxii of the same reference):

The species of Dicranomyia are endemic, and to the five described, others and perhaps many more will, no doubt, be added. They are common insects, sometimes attracted by light and sometimes observed at rest in the daytime, or on the wing in the dark cavity of some hollow tree. In the latter case a number are usually seen flying together, rising and falling in their flight in the narrow space of a few feet. We have bred one or more species from decayed wood, overgrown with damp moss. These fragile flies are the favourite prey of the endemic predaceous wasps of the family Mimesidae, and some of the Crabronidae likewise gather them. Consequently one may find the females of these wasps investigating damp, dark places, where the Dicranomyia are likely to be found, but which ordinarily would have but little attraction for such sun-loving insects.

Writing of the Crabronidae, Perkins says (page lxxxvi of the reference cited):

Xenocrabro hawaiiensis on one occasion was caught carrying off Lispe [Anthomyiidae] and on another occasion a species of the limnobiid Dicranomyia.

De Meijere (1920:59) records *Crabro* (*Rhopalum*) *tibiale* as provisioning its nest principally with *Molophilus armatus* Meij.

Parasitic natural enemies

External parasites

Besides the predatory forms just considered, the various stages of the existence of many crane-flies are threatened with parasites which are equally effective altho more insidious in their method of attack. There are unquestionably many parasites of crane-flies concerning which nothing at all is known at this time. It is inconceivable that such species as *Holorusia grandis*, *Tipula abdominalis*, and other large and common forms do not serve as hosts for parasites as yet unknown. It is this field of investigation that now promises some of the most valuable results.

Hexapoda.— The only parasitic insects of which the writer knows are the dipterous Tachinidae. Glover (1874) states that in Europe certain Tipulae are destroyed by a proctotrupid parasite of the genus Diapria Latreille. Kieffer, in his monograph of the Diapriidae (1911), does not mention this and the writer has not seen it referred to elsewhere. It is probable that the reference pertains to some of the smaller Tipula-like forms of another family. However, it is very strange that one or more of the many families of parasitic Hymenoptera do not infest some stage of the Tipulidae, and it may be confidently predicted that such parasites will one day be discovered.

Tachinidae: Most of the species of the interesting genus Siphona (Bucentes) are parasitic on the caterpillars of various Lepidoptera. Two have been recorded as parasites of the larvae of species of Tipula. The better-known of these is *Siphona cristata* (Fabr.), a constant parasite of the larvae of *Tipula maxima* (Beling 1886, Czizek 1913, Riedel 1913, Thompson 1915). The method of attack by the parasite has been described by Roubaud (1906). The large, massive larvae of this species of crane-fly are amphibious or semi-aquatic, living near the margins of streams and other bodies of water. They live in the mud or in the water beneath the surface, at times coming up to breathe the air thru the two large spiracles at the posterior end of the body. It is at this time, when the spiracular disk is projected thru the surface film and the spiracles are open, that the tachinid is supposed to dart down and deposit its eggs in the open stigmata. The young parasite is somewhat elongated, yellowish orange in color, and about a millimeter in length, and is completely inclosed in a firm, membranous cyst. It is connected with one of the two principal tracheal trunks of the host by a sort of chitinized calyx which opens into the trachea. At the time of their pupation the parasites detach their organs of fixation, and with their heads perforate the skin of the host and enter the humic earth. In nature this departure coincides almost exactly with the time of leaving the water by the host for the purpose of pupation in the earth. The pupal duration of the parasite is about three weeks. Rennie (1912) gives *Siphona geniculata* (De Geer) as a parasite of an undetermined species of Tipula.

Species of the genus Admontia are important parasites of the larvae of crane-flies. In Europe, *Admontia amica* (Meig.) is parasitic on species of Tipula, while in America *A. pergandei* Coq. is an important parasite of the smoky crane-fly, *Tipula cunctans* (Hyslop, 1910:128). In the collection of the Illinois Natural History Survey are several specimens of *A. pergandei* bred from larvae of the smoky crane-fly (larvae taken at Urbana, Illinois, parasites emerged October 9 to 25, 1900). Averin (1913) and Lutchnik (1916), in Russia, record the larvae of a Tipula, in one case at least — that of the economic species *T. oleracea* — as being very heavily infested by an undetermined tachinid which may have been the Admontia species mentioned above.

A third genus of Tachinidae, Sturmia, has recently been reported to the writer by J. D. Tothill as being parasitic on the larva of a large crane-

fly, undoubtedly a tipuline form. The larva was found at Chelsea, near Ottawa, on May 27, 1906, by Dr. James Fletcher, the parasite issuing on June 27. The tachinid is to be described as *Sturmia tipulensis* Tothill.

The genus Trichoparia is parasitic on Ctenophora and its allies.

Altho the Tachinidae are the only dipterous parasites that are definitely known from the Tipulidae, the writer has a record of a species of Phaonia, of the family Anthomyiidae, which possibly is a parasite. Among some Diptera sent to Malloch for naming was one specimen of a Phaonia bearing the label "Bred from tipulid pupa, acc. no. 14022." The writer is indebted to R. H. VanZwaluwenburg for the following facts concerning this specimen: The material was taken by Harry L. Parker on June 6, 1916, on South Mountain, near Hagerstown, Maryland. Under litter and growth of Virginia creeper on rock a tipulid pupa was found. The pupa had been eaten out inside and there was a hole in the side of its body. About a half inch away from this pupa was found a newly formed pupa of an anthomyiid fly. The adult emerged on June 23, 1916, and was pinned. It is possible, of course, that the Phaonia was merely feeding on the tipulid, as recorded for this genus elsewhere in this paper (page 728), and that the species is a predatory enemy rather than a parasite.

Arachnida.— Young mites of species of Trombidium, Rhyncholophus, and other genera of Arachnida, are frequently found attached to the body and the wings of adult crane-flies. This attachment is by anal filaments, and it is doubtful whether any real injury results to the host therefrom. These cases are probably instances of phoresy to provide a means of dispersal of the mite. At various times the writer has found in northeastern America a large number of adult crane-flies so infested, and practically every genus and many species are included among the number.

Fungi.— Among the enemies of crane-flies, both to the immature and to the adult stages, probably none are more lethal in their action than certain parasitic fungi. The largest groups of insect-fungous parasites are the Entomophthoraceae (Phycomycetes) and the Laboulbeniaceae (Ascomycetes). Dr. Roland Thaxter informs the writer that, altho the latter group infest other Diptera, he has never seen specimens on Tipulidae, and none have been recorded in the literature. The writer is greatly indebted to Dr. Thaxter and to A. T. Speare, Government Mycoentomologist, for data on this subject. Dr. Thaxter sent to the writer for determination a considerable number of specimens of crane-flies with their para-

sites, these including the types of many of his Entomophthoraceae and some new species not yet described. From these data and the literature the following notes may be given:

Class, Phycomycetes
Family, Entomophthoraceae

1. *Entomophthora* (*Empusa*) *pachyrrhinae* Arthur. On the larvae of *Nephrotoma ferruginea*; a manuscript name.
2. E. (E.) *sepulchralis* (Thaxt.). On an adult Tipula of the *subunicolores* group.
3. *E.* (*E.*) *caroliniana* (Thaxt.) [= *E. arrenoctona* Giard]. On an adult male of *Tipula entomophthorae.*
4. *E.* (*E.*) *arrenoctona* Giard. On male adults of *Tipula paludosa* (Giard 1888, Villeneuve 1910, Picard 1913).
5. *E.* (*E.*) *tipulae* Fres. On *Tipula maxima* (Lohde, 1872).
6. *E.* (*E.*) *conglomerata* (Sorokin). A species which is probably this one is recorded by Thaxter on larvae and adults of Tipulidae.
7. *E.* (*E.*) *sphaerosperma* Fres. Recorded by Thaxter from adult Tipulidae.
8. *E.* (*E.*) *grylli* Fres. Recorded on at least two occasions from the adult flies of *Tipula ultima* Alex. [= *T. flavicans* Fabr.].
9. *E.* (*E.*) *punctata* Thaxt., ms. On adult females of *Pseudolimnophila noveboracensis.*
10. *E.* (*E.*) *dipterigena* (Thaxt.). On the adult flies of several genera of Limnobiinae, as follows: *Molophilus hirtipennis*, *Limnophila aprilina*, *Pseudolimnophila nigripleura*, *Ulomorpha pilosella*, *Penthoptera albitarsis.*
11. *Isaria* sp. On adults of *Dicranomyia pubipennis.* Additional undetermined species of this same genus on various tropical Tipulidae.

Class, Hyphomycetes.
Family, Mucediniaceae.

12. *Sporotrichum densum* Link. On *Tipula cunctans* Say [= *T. infuscata* Lw.] (Hyslop, 1910:130).

Internal parasites

Crane-fly larvae and adults are infested by numerous protozoan and bacterial parasites, the more conspicuous and constant being the Sporozoa (Gregarinidae) and the Bacteria. General references to this subject may be found in Léger (1892), Labbé (1899), and Minchin (1903). More especial references are made to the parasites of Ptychoptera by Léger and Duboscq (1909), to those of Dicranota by Miall (1893: 237), to those of Ctenophora by Anthon (1908:542), and to those of Tipula by Mackinnon (1913). In the case of Ctenophora the parasites were frequent between the cells of the alimentary canal, especially in the proventricular caeca. The writer has found a large gregarine very abundant in the alimentary canal of the larva of *Pedicia albivitta*, many of the individuals being very heavily infested. Gamkrelidze (1913 b) records gregarine and nematode parasites in Gnophomyia larvae.

The more important recorded protozoan parasites are as follows:

Class, Sporozoa.
Subclass, Telosporidia.
Order, Coccidiomorpha.
Family, Adeleidae.

1. *Adelea tipulae* Léger. In the intestine of species of Tipula.

Order, Gregarinida.
Family, Gregarinidae.

2. *Hirmocystis polymorpha* (Léger, 1892: 113). In the intestine of the larva of *Limnobia* sp.
3. *H. ventricosa* (Léger, 1892 : 111). In the alimentary canal of *Tipula oleracea*, *Nephrotoma pratensis*, and other species.
4. *Gregarina longa* (Léger, 1892:117). In the alimentary canal of a species of Tipula.

Family, Actinocephalidae.

5. *Actinocephalus tipulae* Léger (1892: 141). In the alimentary canal of Tipula larvae. Probably the same species has been recorded from the larvae of a species of Ctenophora.
6. *Pileocephalus striatus* Léger & Duboscq (1909: 887–893). In the mid-intestinal epithelium of the larva of *Ptychoptera contaminata*. The Pileocephalus live in the epithelium of the mid-intestine, attaching themselves to the epithelial cells and hypertrophying the adjoining tissues. They obtain their nutriment from the food that penetrates into the cells.

Family, Stylorhynchidae.

7. Near Stylorhynchus (Miall, 1893: 237). In the stomach of larvae of *Dicranota bimaculata*.

Subclass, Neosporidia.
Order, Cnidosporidia.
Suborder, Microsporidia.
Family, Nosematidae.

8. *Nosema strictum* Monz. (Moniez, 1887). In muscles, conjunctive tissue, and other parts of *Nephrotoma pratensis*.
9. *Gurleya francottei* Léger & Duboscq (1909: 894). In the epithelium of the mid-intestine of the larva of *Ptychoptera contaminata*.

Class, Flagellata.
Family, Trypanosomidae (Herpetomonadidae).

10. *Crithidia campanulata* Léger. At the juncture of the mid- and hind-intestines in the larva of *Ptychoptera contaminata* (Léger & Duboscq, 1909: 898–900).

The writer is indebted to Dr. R. Kudo for assistance in determining the terminology used above.

Bacteria are frequently found in crane-fly larvae. Léger and Duboscq (1909: 900–901) record undetermined spirochaetes in the epithelial cells of the posterior part of the mid-intestine of *Ptychoptera contaminata*. Dr. Hugh Glasgow, of the Geneva Experiment Station, informs the writer that in Illinois a large tipulid larva, probably that of *Tipula abdominalis*, living in the leaf-drift of prairie streams, is heavily infested with bacteria. Most of the specimens observed had an abundance of small coccus and spirochaete forms, with occasional specimens of a gigantic bacillus measuring from forty to eighty microns in length and disporous. These large bacilli infest the hind-gut of the larva.

HISTORICAL SUMMARY OF THE IMMATURE STAGES

The discovery and description of the immature stages of crane-flies has by no means kept pace with the taxonomic work that has been done on the adult flies. There are a very large number of common species in every country concerning whose early stages nothing at all is known, and the knowledge that exists concerning a comparatively small number results from the labors of a few students. Among these may be mentioned Beling, Mik, Brauer, Hart, Needham, and Malloch. Some other workers have given excellent descriptions of single species, while still others have contributed important treatises on the anatomy, morphology, histology, and related subjects of the different species. The descriptions of the earlier workers are, for the most part, of historical interest only, but in a few cases they are exceptional and are still the main source of information concerning certain species. Many of the foremost workers on the taxonomy of the adult flies have summarized the earlier writings on the immature stages but have themselves contributed little to the subject, among these being Schiner, Loew, Osten Sacken, Skuse, and Brunetti. The following chronological summary gives an indication of the more important work that has been done on this phase of the subject:

1722	Frisch	*Tipula oleracea*
1740	De Réaumur	Ptychoptera, Tipula
1776	De Geer	Phalacrocera, Ctenophora, Tipula
1803	Schellenberg	Cylindrotoma
1829	Stannius	*Limnobia xanthoptera* [=*bifasciata*]
1832 (Posthumous)	Lyonet	Ptychoptera
1833	Bouché	*Dictenidia* sp., *Tipula* sp.
1834	Von Röser	*Hexatoma nigra*
1838	Boie	Cylindrotoma
1840	Dufour	Trichocera
1842	Zeller	Cylindrotoma
1846	Bremi-Wolf	Trichocera, *Limnobia xanthoptera* [=*bifasciata*], Nephrotoma
1849	Perris	Trichocera, *Limnophila dispar*, Ula, Tanyptera
1854	Brauer, Egger, and Frauenfeld	Chionea
1867	Nowicki	*Dactylolabis wodzickii*
1872	Weyenbergh	Ctenophora, Dictenidia: anatomy and histology
1873–86	Beling	The immature stages of 69 species of European Tipulidae, including 30 species of Tipula
1875–76	Hammond	*Tipula oleracea*: anatomy
1876	Grobben	Ptychoptera: anatomy
1876–1902	De Rossi	*Liogma glabrata*, *Tanyptera atrata*
1880	Hermann	*Tanyptera atrata*
1882–1900	Mik	Discobola, Elliptera, Dactylolabis, *Tipula rufina*, etc.

1883	Brauer	Important work on the classification of the immature stages
1884	Gercke	*Rhamphidia longirostris*, *Tanyptera atrata*
1890	Van Gehuchten	Ptychoptera: histology of alimentary canal
1893–97	Miall	Dicranota, Phalacrocera
1895 [1898]	Hart	Pioneer American worker; Bittacomorpha, etc.
1897	Bengtsson	Phalacrocera: anatomy
1900–09	Johnson	Teucholabis, Aeshnasoma, etc.
1901	Kellogg	*Holorusia grandis* (as *rubiginosa*): anatomy
1901	Müggenberg	*Liogma glabrata*
1901–08	Needham	*Dicranomyia simulans*, *Pedicia albivitta*, Rhaphidolabis, *Tipula ultima* (as *flavicans*)
1907–08	Steinmann	*Triogma trisulcata*
1908	Holmgren	Phalacrocera: mouth parts
1908	Anthon	*Ctenophora angustipennis*: anatomy
1908–09	Pastejrík	*Limnobia xanthoptera*, Ctenophora
1908–09	Müller	*Triogma trisulcata*
1909	Brocher	*Tipula lunata*
1909	Greene	*Tipula trivittata*
1909	Thienemann	*Dicranomyia trinotata*
1910	Brown	*Tipula maxima*: anatomy
1910	Hyslop	*Tipula cunctans* (as *infuscata*)
1911	Vimmer	Ctenophora, *Tipula oleracea*: mouth parts
1911–16	De Meijere	*Trentepohlia pennipes*, *Tipulodina pedata*, and several European species
1912	Keilin	Trichocera: morphology
1913	Caudell	*Tipula ultima* (as *flavicans*)
1913	Gerbig	Anatomy of the respiratory system of many European species of Tipulidae
1913	Picado	*Trentepohlia bromeliadicola*
1914	Del Guercio	*Tipula oleracea*
1914–16	Topsent	*Ptychoptera albimana*
1914–19	Alexander	Dicranoptycha, Ula, Eriocera, Hexatoma, Penthoptera, Liogma, Prionocera, *Tipula arctica*
1915	Swezey	*Dicranomyia foliocuniculator*
1915	Lovett	*Ctenophora angustipennis*
1915	Wesenberg-Lund	Dicranota, Phalacrocera, Triogma
1915–17	Malloch	*Limnobia immatura*, Gnophomyia, and, in his uncertain material, Antocha, Elephantomyia
1916–17	Rennie	*Tipula paludosa*
1918	Cameron	*Cylindrotoma splendens*
1920	Hudson	*Gnophomyia rufa*, *Limnophila sinistra*
1920	Lenz	Thaumastoptera, Cylindrotominae

ECONOMIC IMPORTANCE

The larvae of some species of crane-flies, almost all belonging to the genera Tipula and Nephrotoma, often do considerable damage to various crop species, the injury being largely caused by the larvae devouring the roots and thus killing the plants. Certain of these crane-fly species, as *Tipula oleracea*, *T. paludosa*, and *Nephrotoma maculata* in Europe, and *Tipula bicornis* and *Nephrotoma ferruginea* in America, have long been known, but several others have come into prominence only within the

past ten years, notably *Tipula parva* Lw. (supposition) in Japan, and *T. cunctans* and *T. simplex* in North America. The more important outbreaks of this nature which have been recorded are as follows.

Species affecting herbaceous plants

Nephrotoma ferruginea has been reported by Webster (1891, and 1893 a: 243–245) as injuring young wheat in Indiana, the injury in some cases being estimated at fifty per cent.

Tipula oleracea is the best-known European species in this group, infesting a wide range of plants. The more important outbreaks of this species as recorded are as follows: Ewert (1899) reports from Germany an unusually severe attack, in which the larvae of this species and of *Tipula nigra* did a considerable amount of damage to the roots of grasses. They were so abundant that from ten to twenty could be found in the area of one square foot. Grasses in the infested area were completely destroyed. Ormerod (1885, 1886, 1900) records serious injury by *T. oleracea* to pastures and meadows in England, and recommends applications of guano either alone or mixed with salt, kainit, or superphosphate. This species has been recorded also as being a serious pest in Ireland (Anonymous reference, 1904 b) in grainfields and meadows, and careful plowing and the use of fertilizers for its control are advised. Schoyen (1903), in Norway, reports serious injury to meadows and pastures, as well as to cereals and young cabbage plants. Del Guercio (1914) records serious injury in the Italian rice fields.

A few additional outbreaks of *Tipula oleracea* may be mentioned. Barthou (1913) records injury to canes (raspberry, strawberry, and others) in France. Désoil (1914) reports injury to meadows in France, and Ritzema Bos (1915) to meadows in Holland.

Tipula paludosa is reported by Lind, Rostrup, and Kolpin Ravn (1914 and 1915) as causing serious injury to oats and barley in Denmark, and Rennie (1916 and 1917) reports the same species as injuring corn and pastures in England.

Tipula flavolineata is reported by Sopotzko (1916) as injuring clover in Russia. The specific identity, however, is probably erroneous, as this species lives almost entirely in decaying wood (Beling, 1873 b: 581–582).

Onuki (1905) records *Tipula parva* Lw. (supposition) as one of the serious rice pests in Japan. In some localities from sixty to ninety per

cent of the seedlings have been destroyed by this species. The larvae apparently cannot exist in water for any long period of time, and so may be killed by flooding the fields for from six to thirty-six hours. Del Guercio (1914) offers the same recommendation for the control of *T. oleracea* in the Italian rice fields.

Tipula bicornis has been found in grass and clover lands in Illinois by Forbes (1890), and on clover in Indiana by Webster (1892 a).

Tipula cunctans, as recorded by Hyslop (1910:126, as *T. infuscata*), works largely on Japan clover and other leguminous plants. The larvae are often exceedingly numerous, as many as two hundred having been found in an area covering but little more than one square foot of soil. They destroy the plants by devouring the roots and sucking the juices. It is recommended that the infested fields be plowed under before the adult flies emerge (in the autumn), and the following season be planted to corn or potatoes or else left fallow.

Tipula simplex has been found on pasture land and alfalfa in California by Doane (1908) and by Carnes and Newcomer (1912). Doane (cited by Hyslop, 1910:120–121) also reports an outbreak of this species on wheat and grass lands and in clover fields in central California in 1907, and states that thousands of acres of these crops were stripped of their verdure.

The following summary gives the various species of plants that are damaged or destroyed by crane-flies in general. Very many of the injuries reported for *Tipula oleracea,* however, are omitted.

Family	Crop	Species	Authority
Gramineae	Wheat	*Nephrotoma ferruginea*	Webster (Indiana), 1891, 1893 a
	Wheat	*Tipula simplex*	Hyslop (California), 1910
	Wheat	Tipulidae	Stedman (Missouri), 1902
	Corn	*Tipula paludosa*	Rennie (England), 1917
	Corn	*Tipula* sp.	Kirk (New Zealand), 1895
	Barley	*Tipula paludosa*	Lind, Rostrup, and Kolpin Ravn (Denmark), 1915
	Barley	*Tipula* sp.	Wahl and Müller (Germany), 1914
	Barley	*Tipula oleracea*	Goriatchkovsky (Russia), 1915
	Oats	*Tipula paludosa*	Lind, Rostrup, and Kolpin Ravn (Denmark), 1914, 1915
	Rice	*Tipula oleracea*	Del Guercio (Italy), 1914
	Rice	*Tipula parva*	Onuki (Japan), 1905
	Cereals	*Tipula oleracea*	Anonymous reference (Ireland), 1904 b
	Cereals	*Nephrotoma pratensis*	Hollrung (Germany), 1898

Family	Crop	Species	Authority
Gramineae	Meadows and pastures	*Tipula bicornis*	Forbes (Illinois), 1890
	Meadows and pastures	*Tipula simplex*	Carnes and Newcomer (California), 1912
	Meadows and pastures	*Tipula oleracea*	Anonymous reference (Ireland), 1904 b
	Meadows and pastures	*Tipula oleracea*	Désoil (France), 1914
	Meadows and pastures	*Tipula paludosa*	Rennie (England), 1917
	Meadows and pastures	*Tipula* sp.	MacDougall (Scotland), 1915
	Meadows and pastures	*Tipula* sp.	Ritzema Bos (Holland), 1915
	Meadows and pastures	*Tipula* sp.	Marchal and Prillieux (France), 1916
	Meadows and pastures	*Tipula oleracea*	Ormerod (England), 1885, 1886, 1900
Liliaceae	Tulips (bulbs)	*Nephrotoma maculcta*	Collinge (England), 1911
	Onions and garlic	*Tipula oleracea*	Vassiliev (Russia), 1915
Cruciferae	Cabbage	*Tipula oleracea*	Schoyen (Norway), 1903
	Cabbage	*Tipula oleracea*	Averin (Russia), 1913
	Cabbage	*Tipula oleracea*	Goriatchkovsky (Russia), 1915
	Cabbage	*Tipula* sp	Lutchnik (Russia), 1916
	Cabbage	*Nephrotoma* sp	Lutchnik (Russia), 1916
Polygonaceae	Buckwheat	*Tipula oleracea*	Goriatchkovsky (Russia), 1915
Rosaceae	Roses	*Nephrotoma lineata*	Schaufuss (Germany), 1901
	Raspberry and strawberry	*Tipula oleracea*	Barthou (France), 1913
Leguminosae	Clover	*Tipula bicornis*	Webster (Indiana), 1892 a
	Clover	*Tipula bicornis*	Forbes (Illinois), 1890
	Clover	*Tipula flavolineata*	Sopotzko (Russia), 1916
	Clover	*Tipula oleracea*	Del Guercio (Italy), 1914
	Japan clover	*Tipula cunctans*	Hyslop (Tennessee), 1910
	Alfalfa	*Tipula simplex*	Carnes and Newcomer (California), 1912
	Peas	*Tipula paludosa*	Lind, Rostrup, and Kolpin Ravn (Denmark), 1914
Umbelliferae	Carrots	Tipulidae	Lesne (France), 1905
Solanaceae	Potatoes	*Tipula oleracea*	Beling (Germany), 1887
	Potatoes	*Tipula lateralis*	Cameron (Scotland), 1917
	Potatoes, stored	Trichocera	Johannsen (Maine), 1910
	Potatoes, stored	Trichocera	Carpenter (Ireland), 1912
Compositae	Cardoon	*Tipula* sp	Lesne (France), 1908

Species affecting woody plants

Species that injure or destroy living trees or shrubs are not common, and the damage that they do is almost entirely of a minor nature.

Ctenophora angustipennis is recorded as doing secondary damage to prune trees in Oregon (Lovett, 1915). Fuchs (1900) records four species — *Tipula scripta*, *T. marginata*, *Nephrotoma cornicina* [as *iridicolor*], and *N. quadrifaria* — as injuring young plants of both deciduous and coniferous species. Taschenberg (1880:54) describes *Tipula flavolineata* and *Nephrotoma crocata* as destroying year-old seedlings of fir and larch. Matsumura (1916:466) records the larva of *Nephrotoma makiella* as injurious to the mulberry (Morus) in Formosa.

METHODS OF EXPERIMENTAL PROCEDURE

Collecting

The larvae of the larger species of crane-flies, such as those of the genera Tipula, Pedicia, and Eriocera, may be readily discovered in the field, but the immature stages of the smaller Tipulidae are not so easily found. It is necessary to bring into the laboratory large quantities of the material in which the immature stages are supposed to be living, and there to examine it with considerable care. In the case of mud or earth, it is better to wash away the finer silt particles and examine the residue. The writer has found it most convenient to use a Simplex water-net, placing in it a handful of earth and holding it underneath a running faucet. The mesh of this net is of sufficient diameter to retain any crane-fly larvae except the very young stages. When the fine particles have been removed the residue can be examined in water in white enameled or porcelain dishes, and the larvae and pupae may be easily detected in the water. Numerous associated forms of life will be found, and these should be preserved or recorded.

The immature stages of wood-inhabiting species are most easily found in the field by a patient and painstaking examination of the removed bark and the exposed parts of the tree stump or trunk. Moss-inhabiting species, such as those of Liogma and many tipuline forms, may be shaken from their haunts onto a piece of white oilcloth, where they are easily observed.

Killing and preserving

The larvae and pupae to be studied should be dropped into boiling water for a brief instant. The larva, on contact with the water, at once expands to its maximum size, the spiracular disk is spread wide open, and the anal

gills are completely everted. The specimens should be placed in 4-per-cent formalin or, preferably, 70- to 75-per-cent alcohol. Large, fleshy larvae, such as those of the Tipulinae, should be slit at the third or the fourth abdominal segment to allow easy penetration of the preservative. Other notes on preserving material are given by Banks (1909) and by Williamson (1916).

Study

In the study of the gross material, both the binocular and the compound microscope may be used. A special word on the preparation of the head capsule of the larva may be helpful. In removing the head capsule from the body it is generally easiest to slit longitudinally the thoracic segments back of the head and pull the capsule thru this incision. In forms with compact and massive capsules, the thorax and the head may be snipped off and the head everted after the manner of turning the finger of a glove. The capsule should be left in a 5-per-cent solution of caustic potash until all the fleshy parts have been removed. It should be dissected out so that all the mouth parts are isolated and rendered distinct for study. Then follow the usual processes of washing and dehydration, and the final mounting in canada balsam.

Various means are available for examining the spiracular disk. The specimen may be placed in a watch crystal under water and held firmly in place by a piece of glass, as, for example, a broken microscope slide. By holding a heavy piece of glass over the anterior end of the body, the posterior end may be bent at a right angle and bolstered in place by two or three other glass fragments so that the disk is directed straight upward and its details are easily examined. Other methods, such as embedding the anterior end of the larva in paraffin in a deep dish and submerging the body, may be followed. It must be emphasized that in alcoholic gross material the study should be conducted under alcohol or water.

The measurements of the pupa — abbreviated in the text as *d.-s.* (dextro-sinistral) for the width and *d.-v.* (dorso-ventral) for the depth — are taken opposite the wing pad.

Rearing

In order to rear the immature stages of crane-flies successfully the natural haunts should be imitated as closely as possible. In the case of wood-inhabiting species, large pieces of the material in which the larvae

are working may be brought into the laboratory and placed in the breeding cages. This method may be followed with species of Tanyptera, Ctenophora, and other genera.

Fungicolous species, as a rule, also are easily reared. The entire fungus in which the specimen is found should be brought into the laboratory and placed in a jar on a bed of clean sand. The sand takes up the liquids produced by the disintegration of the fungus and provides a place for pupation. Species of Limnobia, Ula, and other forms are reared in this manner.

The chances for error in rearing are many. One must be certain that there are no other larvae in the breeding jar with the one that is being reared; else one of these other larvae might transform and emerge first, and the results would be altogether misleading. The writer has had this happen in his breeding cages, even after the utmost care had been used to guard against it. Beling, the great German student of the immature stages of crane-flies, made a few mistakes in the same way; as, for example, in the case of his Trimicra, the larvae that he describes being pediciine and probably a species of Dicranota or the young larvae of a Tricyphona. What happened, presumably, was that Beling found these pediciine larvae and placed them in rearing; in the same cage, but unknown to the breeder, was a larva of Trimicra which emerged, and naturally Beling thought it came from one of the larvae that he had placed in rearing. It is usually easy to check up such errors. Thus, the writer has placed in rearing the larvae of Penthoptera and, to his surprise, had adults of *Limnophila adusta* emerge. Obviously larvae of *L. adusta* got into the cage in spite of precautions, and emerged first. When closely related species are concerned, however, it becomes a hard matter to straighten the tangle. Hence a species cannot be reared too many times, since each rearing checks up the previous results.

The precaution to be taken in the case of mud-inhabiting or sand-inhabiting species is to see that the mud or sand is baked or thoroly desiccated in order to destroy all life in it. Then it may be remoistened, and the larva or larvae chosen to rear may be put into the earth without the chance that some unknown larva may be lurking in the medium and may emerge first, and so bring about confusion.

The writer has found that the most satisfactory way to rear small tipulid larvae found in earth or sand is to place a small amount of baked

earth from their haunts in a 4- or 6-dram shell vial, moisten the earth, and place a thin layer of moss over it. The vial should not be corked, but should be covered with a piece of cheesecloth held in place by rubber bands. In the case of carnivorous species, as the Hexatomini and the Pediciini, individuals should be isolated in vials, but the herbivorous species may be bred in large numbers in single containers. The predatory forms are usually distinguished without difficulty by their extremely active, snakelike motions, the other species being more sluggish in their actions.

Strictly aquatic forms, such as Antocha, are reared only with great difficulty. These species can survive only in rapidly flowing, well-aërated water, and it is usually a difficult matter to imitate this condition successfully. The best plan is to place rearing cages in the natural haunts of the larvae. This can be done if a suitable location is sufficiently close at hand and free from disturbance by inquisitive passers-by. The chief source of danger to breeding cages in natural streams is that a sudden rise of water may suffocate the larvae or wash the cages downstream, or else may destroy the contents of the cage by a thick deposition of silt. Lotic species that are discovered in streams far removed from the laboratory can be transported alive for long distances in folds of wet cheesecloth. The writer has found this to be the most satisfactory way to keep advanced pupae alive until they are ready to emerge as adults.

In general, the writer has found species of the tribe Pediciini the most difficult to rear, and the Limnobiini and the Eriopterini perhaps the easiest. Mud-inhabiting species are easily reared, but species from rushing torrents are at the opposite extreme and it is almost an impossibility to bring some of these species thru to the adult condition.

TYPES OF THE IMMATURE STAGES

The material on which this study is based was almost entirely reared. It seems desirable that these authentic specimens of the larva and the pupa should be so designated that they will have a value greater than that possessed by ordinary specimens. No terms for the designation of types of the immature stages are known to the writer, and the two that are needed in this paper are here defined as follows:

Nepionotype, The type of the larva.

Neanotype, The type of the pupa.

The type specimen should, of course, be selected only when there is absolute certainty of the identification, and in most cases this determination can be made only by rearing the species. After the species has been reared (this should be done many times, if possible, in order to check up the identity), a good representative specimen may be chosen as the type of the stage. In the cases in which the species is known only from a single specimen, the nepionotype may be the larval skin, the neanotype the pupal skin. The remaining specimens of the original series become paratypes. The types of the immature stages possess fully the value of the type of the adult and should be as carefully preserved. The types herein designated are in the collection of the writer. They are preserved in alcohol, but the larval heads of most species have been removed, treated with caustic potash, and mounted in balsam.

EXTERNAL MORPHOLOGY

The larvae and the pupae of crane-flies show considerable diversity in their general form. The fundamental plan of structure remains much the same thruout the group, but the details are widely different and furnish the characters in use for the separation of the various tribes and lesser divisions.

The immature stages of crane-flies have evolved more rapidly than have the adult flies, and in many features they show a greater specialization. The head capsule of the larva seems to be the most constant feature, the same fundamental type of structure recurring in the generalized members of all the various groups, indicating a close phylogenetic relationship. On the other hand, the respiratory organs of both the larvae and the pupae vary greatly in the different species and are obviously molded by habitat. The often-repeated statement that the inside of an organism shows what it is, while the outside shows where it has been, is well illustrated here.

The larva

General features

The form of the larval body is, as a rule, moderately elongated and usually terete. The head is eucephalous and non-retractile in the three families Tanyderidae, Ptychopteridae, and Rhyphidae. It is incomplete and more or less retractile in all the species of Tipulidae. The body is shortest in the more generalized forms, becoming greatly elongated

in many Eriopterini and some Limnobiini (Dicranoptycha). It is made up of the composite head capsule, three thoracic segments, and nine evident abdominal segments. In some species all the abdominal segments are subdivided, respectively, into a narrow basal and a usually broader posterior ring, or annulus; in other species only the basal segments are so subdivided. The integument is usually covered with a dense appressed pubescence and often bears setae, or pencils of hairs, or, in some Cylindrotominae, spinous projections.

Respiration is characteristically metapneustic; in the Rhyphidae it is amphipneustic, in Antocha apneustic. The typical metapneustic forms often show vestigial lateral spiracles, but these are not functional in any species known to the writer and the peripneustic type of larva is still unknown in this group of Diptera. The spiracles are placed at the ends of the long breathing tubes in the Tanyderidae and the Ptychopteridae. In the Tanyderidae, the Tipulidae, and the Rhyphidae the disk is surrounded by a varying number of lobes which are rarely indistinct, these ranging in number from two to eight. Anal gills are found in representatives of almost all the major groups of crane-flies, and their loss is a result of habitat and non-usage. In wood-inhabiting species the gills are often modified into blunt lobes, having the evident function of propulsion by shoving.

Body form

As already stated, in the majority of crane-fly larvae the body is terete or approximately so, but in some species it is decidedly depressed with the ventral surface flattened. Such forms are Dactylolabis, some Cylindrotominae, and some Tipulinae. The integument is produced into elongate spines and blades in almost all species of Cylindrotominae, similar conditions being suggested in a few tipulines. A definite arrangement of setae (chaetotaxy) obtains. The basal abdominal ring is provided with a transverse creeping-welt in the Limnobiini and in some Hexatomini and Pediciini, as well as in a few other forms. In some genera, as Epiphragma, this welt is practically naked; in others it is covered with a microscopic scurfiness; while in still others (Dicranota) it is separated into distinct paired prolegs, which are armed with circlets of chitinized hooks that lessen in size from the tips basally. The welts are both dorsal and ventral in position in many Limnobiini and in some Pediciini (Rhaphi-

dolabina), or are ventral only (Rhamphidaria, Ularia, Epiphragmaria, and most Pediciini). In number they range from four (on abdominal segments 4 to 7) in most Pediciini, to five or six (on abdominal segments 2 to 7) in Ularia, Epiphragmaria, and other forms.

Organs of respiration

The spiracular disk.— The posterior end of the body is usually truncated, bearing the two spiracles and surrounded by a number of fleshy lobes. These lobes vary much in their shape and armature, and range in number from two in the Pedicaria and the Antocharia to six or eight in the Tipulinae. The inner faces of the lobes are often lined with brown or black horny plates, which serve as points of attachment for the longitudinal muscles. Their arrangement and distribution are of great service in specific classification.

The Limnobaria usually have the lobes surrounding the spiracular disk indistinct; the Antocharia have two long ventral lobes; the Rhamphidaria five lobes; the Ellipteraria and the Dicranoptycharia four lobes.

In the Eriopterini, the Elephantomyaria and some Eriopteraria have four lobes; the majority of species of the latter division have five. In these last-named species the disk is almost squarely truncated, and the five lobes are subequal and stellate in appearance.

The Hexatomini usually have four lobes, with the ventral pair longer than the lateral pair. In a few cases only (Ularia, Dicranophragma, Poecilostola), a reduced mid-dorsal lobe is present. In the more specialized forms the lateral lobes also tend to reduce, simultaneously with the elongation of the ventral lobes. In this tribe the disk is fringed with long hairs, which are sometimes excessively elongate, especially on the ventral lobes where they appear as long fringes of delicate hairs that spread out on the surface film of the water as broad fans. Such fringes are found in a large number of Hexatomini and also in the Adelphomyaria (supposition). Near the tips of the ventral lobes, but inside this fringe of hairs, are often inserted one or more stiff sensory bristles.

In the Pediciini, the Pedicaria have two lobes and the Adelphomyaria (supposition) have four. In the former division the lobes are ventral in position and are almost naked.

The Cylindrotominae have six rather indistinct lobes in Cylindrotoma, and four in the other genera.

The Tipulinae show six lobes in practically all genera, the only exceptions being that there are eight in a few rare cases of Tipula and five in Dolichopeza, and that lobes are indistinct or lacking in Tanyptera.

In the Rhyphidae (Trichocerinae) the spiracular disk is very similar to that in many Tipulidae, and is surrounded by four lobes. In the Ptychopteridae the very reduced disk is borne at the tip of a slender, retractile breathing tube. In the Tanyderidae the condition is somewhat similar, but here the disk is larger and is surrounded by five lobes at the tip of a long, stout, non-retractile breathing tube.

The spiracles vary greatly in size from very large to small and vestigial, or they may even be lacking in some species of Antocha. They consist of an apparently uniform middle piece surrounded by a radially folded margin, or ring, of various widths, called the *stigmal ring*. Many authors (De Meijere, Mik, Müggenberg, Brown, Keilin, and others) hold that the middle piece is an imperforate chitinized plate and that respiration takes place thru the stigmal ring. Gerbig (1913), however, shows that the middle piece is split across the disk, the cleft being closed by two overlapping membranes. Directly behind the spiracles the tracheae enlarge into the felt chamber, whose walls are provided with long, branched, treelike structures, the branches apparently anastomosing. Surrounding the felt chamber in many larvae are dense masses of air tubes, which make up the tracheal lungs. These tubes are arranged in bundles, which arise in special cavities of the felt chamber; thus, in *Tipula paludosa*, there are about fifty bundles, each of about twenty tubules, making a total of one thousand of these air canals (Gerbig).

The early stages of the larva are quite different from the later developmental stages, as Gerbig (1913:137–140), working on *Tipula paludosa*, has well shown. The prominent six-lobed spiracular disk of the more matured larva is represented in the first developmental stage by four heavily chitinized projections, which bear but few bristles on their outer margin. The dorsal lobes are not evident, but are replaced by eight branched bristles, about equidistant from one another. The spiracles are oval, not circular as in the grown larva, and project a little beyond the level of the disk. The writer has noted several first-stage larvae with an appearance almost as described but showing several points of difference. The immature larvae of Phalacrocera are described elsewhere in this work (page 963).

Anal gills.— In the Ptychopteridae and in the Tanyderidae there is but a single pair of anal tracheal gills. In the former these are very small and are cylindrical, in the latter they are large, branched, fanlike structures. In the Tipulidae the anal gills number from four in most Limnobiinae to six or eight in the Tipulinae. The increase in number is brought about by a division of the original gill of each side. In generalized forms, as Antocha, Pedicia, and others, the anal gills are constricted into segments, the apical ones being more or less telescopic into the preceding ones. As a rule the anal gills are entirely or almost entirely retractile within the body.

In the Tipulinae the gills vary with the genera, being blunt and constructed for propulsion in the wood-inhabiting species, such as those of Ctenophora, Tanyptera, Tipula, and other genera. In the semi-aquatic species of Tipula the number of gills varies from four to eight. In the latter case each of the four principal gills is deeply bifid and the gills are arranged transversely, as in *T. ignobilis*; in species with six gills the posterior branches of the posterior gills are atrophied as a rule; in other species, which have but four gills, the four anterior branches are preserved, the posterior pair being usually atrophied. In Longurio and Aeshnasoma the four anal gills are pinnately branched, each with about six lateral branches. A similar condition is found in the Tanyderidae.

The head

The primitive crane-fly head was undoubtedly of the eucephalous, non-retractile type, as found in the Ptychopteridae, the Rhyphidae, and other families. The retracted head capsule of the Tipulidae is a derived condition.

The massive, compact capsule is found in all of the lower groups of the three subfamilies of the Tipulidae. Such a head is easily derivable from the condition in the Rhyphidae or in the Tanyderidae, for instance. The dorsal median sclerite, the *prefrons*, is almost as large and conspicuous in Ula as in the eucephalous families. The lateral plates that constitute the capsule are shaped like a mussel in the generalized groups, with the posterior incisions shallow. In the more specialized forms, with the capsule greatly dissected, the two plates of either side are entirely separated — the innermost, next to the prefrons, being the *internal-lateral* of De Meijere, and the outermost being his *external-lateral*. The prefrons

is found in all forms with the capsule compact and massive, and is even preserved in many species with the dissected capsule. In many cases, however, it is firmly fused with the internal-lateral plates; or, in some cases, all the plates of the capsule are firmly united and their individual limits are ill-defined. In the generalized forms the clypeus and the labrum are entirely distinct from each other, while in other forms the two lose their individuality by fusion.

The sclerites of the generalized primitive head bear bristles, or setae, of various types and arrangement. In the Tanyderidae the punctures are multisetose; in most Ptychopteridae the setae are branched or somewhat plumose.

The literature on the head capsule and the mouth parts is as follows:

Ptychoptera. De Meijere, 1916: 188–191, figs. 14–20.
Bittacomorpha. Hart, 1898 [1895]: 192, pl. 5.
Trichocera. De Meijere, 1916: 191–194, figs. 21–23.
Limnobia. De Meijere, 1916: 198–201.
Dicranomyia. De Meijere, 1916: 197–198, figs. 32–35.
Dicranoptycha. Alexander, 1919 b: 71, figs. 2, 3.
Elliptera. Mik, 1886 b: 339, pl. 6.
Ula. Alexander, 1915 a: 5–6, pl. 1.
Dactylolabis. Mik, 1894: 261–266, pl. 2; Nowicki, 1867: 341 (as Rhicnoptila).
Limnophila. De Meijere, 1916: 204–206, figs. 49–51.
Eriocera. Alexander and Lloyd, 1914: 21–22, pl. 1.
Hexatoma. Alexander, 1915 c: 146, pl. 1.
Penthoptera. Alexander, 1915 c: 155, pl. 1.
Tricyphona. De Meijere, 1916: 195–196, figs. 29–31.
Pedicia. Needham, 1903: 286, fig. 19.
Dicranota. Miall, 1893: 237–238, pl. 10.
Ormosia. De Meijere, 1916: 201–204, figs. 37–47.
Gnophomyia. Malloch, 1915–17 b: 230–231, pl. 34, fig. 10.
Chionea. Brauer, Egger, and Frauenfeld, 1854: 614, pl. 11.
Phalacrocera. Miall and Shelford, 1897: 344–345; Bengtsson, 1897.
Cylindrotoma. Cameron, 1918.
Liogma. Müggenberg, 1901; Alexander, 1914: 111, pl. 1.
Ctenophora. Anthon, 1908: 544.
Prionocera. Malloch, 1915–17 b: 199, pl. 32, figs. 1–3.
Holorusia. Comstock and Kellogg, 1904: 55, 61–62.
Tipula. Vimmer, 1906, and 1911: 1–6.

In addition to the preceding, the genera Helobia (Beling, Hart, Malloch), Rhaphidolabis (Needham), and Tanyptera have been discussed less fully.

All of the above-named genera are considered in this paper, and the head capsule and mouth parts of the following genera are described also: Protoplasa (supposition), Bittacomorphella, Rhipidia, Rhamphidia, Antocha, Epiphragma, Pseudolimnophila, Pilaria, Ulomorpha, Elephantomyia, Teucholabis, Gonomyia, Erioptera, Molophilus, Adelphomyia

(supposition), Rhaphidolabina, Oropeza, Longurio, Aeshnasoma. The descriptions for the genera are either entirely new or else the characters have heretofore been insufficiently described and figured. The details of structure of the head capsules of nearly fifty genera of crane-flies are now known.

The labrum and the epipharynx.— The labrum is preserved in all crane-fly larvae. It is usually broadly transverse or oval. The dorsal surface is clothed with short hairs, these being longer on the anterior margin, which is often provided also with a limited number of sensory bristles, or papillae. The lateral regions on the ventral, or epipharyngeal, side often bear long tufts of hairs. The epipharynx proper is variously armed in the different groups of crane-flies.

The labium.—The labial region of the capsule is of vast importance in classification, and the location of the constituent parts should be early appreciated. The confusion in terminology of the dipterous larval labium has been partly outlined by De Meijere (1916:253). The principal synonyms are as follows:

Submentum.

Mentum — The pharyngeal plate, or lower lip (Meinert); submentum (Miall); ectolabium (Bengtsson); labial plate.

Prementum — Mentum (Miall); ectolabium (Keilin); endolabium (Holmgren, Vimmer, Bengtsson).

Hypopharynx — Labium (Meinert); mentum (Miall, in Dicranota); endolabium (Keilin).

The submentum is represented by a narrow transverse strip in the eucephalous groups of crane-flies, being well shown in Ptychoptera. The mentum is the usually chitinized anterior-ventral plate of the capsule. In Ptychoptera it is margined anteriorly with about twenty comblike teeth. In Bittacomorpha it is more or less distinctly bilobed, but is untoothed. In the generalized Tipulidae it is indistinctly divided into an outer plate and, immediately dorsad of this and closely applied to or fused with it, an inner plate. The outer plate furnishes the apical median tooth of the mentum and in some cases an additional tooth on either side. The inner plate adds a varying number of teeth to the mental plate, from two in Epiphragma to as many as ten or twelve in some species of Limnobia. The chitinized plate is completely divided medially in some Eriopterini (Molophilus and some Erioptera), in the Pediciini, and in some Hexatomini (Pseudolimnophila). In this case, each half is

directly continuous with the ventral bars of the head capsule. In the Limnophilaria the mentum is represented by a narrow, transverse, chitinized bar, which is delicately grooved with parallel lines. The mentum is lacking in chitinized parts, or apparently so, in many Eriopterini and in the higher Hexatomini.

Directly behind the mentum is the prementum, rarely prominent and bearing the two small palpi when they are preserved, as in the Ptychopteridae. The hypopharynx lies immediately dorsad of the prementum. In the Ptychopteridae this is an enlarged, two-horned, fleshy lobe which is difficult to study. In the Tipulidae the generalized condition, such as occurs in the Limnobiini and the lower Hexatomini, consists of two collar-like chitinized plates whose anterior margins bear from ten to fifteen or more teeth. In the Tipulini this plate is narrow, with the anterior margin few-toothed, there usually being five or in some cases six teeth. In the Pediciini the hypopharynx is labriform; in many Eriopterini it is cushion-shaped and covered with numerous blunt setae.

The antennae.— The antennae are borne on the anterior lateral margin of the capsule, laterad of the labrum. They are one- or two-segmented, and in most cases have one or more apical papillae. De Meijere and others hold that the principal apical papilla constitutes an additional antennal segment. In some cases, however, as in Ula for example, two or even more papillae are found which are very similar to one another except for slight degrees of size. It is difficult in such cases to hold any one of these papillae as a true segment. The writer prefers to consider them as apical sensory papillae, and they are so treated in this paper.

The primitive antennae are not greatly elongated, and are usually short-cylindrical or subglobular (Ula). An auditory plate, circular in outline and lying on the face of the basal segment, is almost always present. The apical papilla in the Limnophilaria and the Eriopterini is egg-shaped, or oval, and is delicately sculptured by a network of apparently impressed lines. In many species, as for example those of the higher Hexatomini, the apical papillae are very long, tapering to the tips. In many Limnobiini, as for example Limnobia, and in many species of Tipula and related forms, the apical papilla is button-shaped, or disklike, and is often very reduced.

The mandible.— In the primitive type, such as occurs in the eucephalous groups and in the generalized Tipulidae, the mandible is rather com-

plicated, usually having a considerable number of teeth on the cutting edge and a distinct sub-basal arm (prostheca) or prosthecal tuft of hairs. At the same time there are usually one or more setae on the outside of the mandible, near the "heel," or base, of the scrobal region. In the generalized tipulid type there are two apical teeth and two rows of cutting teeth. In other cases, as in the Limnobiini, there are but a single dorsal tooth, a single apical tooth, and a varying number of cutting teeth on the ventral face; in some species of Limnobia the number of teeth in the ventral cutting row is six or seven. In the Tipulini the mandible is often reduced in size (as in Tanyptera), there being but a single dorsal and a single ventral tooth in addition to the apical point; the prostheca, however, is usually well developed. In the Eriopterini but one row of teeth, the ventral, is strongly developed. In the Pediciini and the higher Hexatomini, the mandible is elongate and sickle-shaped, with the few teeth on the cutting edge at about midlength. In Ulomorpha the mandible is hinged at about midlength, the basal part being hollowed out on the inner face to receive the blade in a position of rest.

The maxillae.— The maxillae are usually of simple form. In the generalized types, such as the eucephalous families and the lower groups of the subfamilies of Tipulidae, they consist of a large and distinct transversely triangular cardo, a conspicuous stipes, and distinct inner and outer apical lobes. In the Pediciini the lobes are separate in the supposed Adelphomyia larva but are fused together in the highest types (Dicranota). In the Hexatomini the lobes are reduced to a single long, flattened blade. The outer and inner lobes are usually densely hairy, especially at the tip and on the inner face of the latter. The palpus is uni-articulate and antenniform in the generalized forms, is short-cylindrical with a varying number of tiny sense pegs at the apex, and bears on its face a circular auditory plate similar to that of the antenna. The armature of the inner lobes is varied, in some species being provided with stiff, comblike setae, or projections.

The pupa

General features

The pupa of the crane-fly is of the so-called "free," or "mummy," type. In only a few cases does the larval skin adhere to the end of the abdomen (Dactylolabis, Cylindrotoma, and some other forms.) The head is usually small, and is ventral in position. Immediately behind the

head on the pronotum are the two breathing horns, which are variously developed in the different tribes and genera and furnish invaluable bases for classification. The leg sheaths usually far exceed the short or but moderately elongate wing sheaths. The abdominal segments are often provided with a subterminal armature of stiff setae, or spines. At the posterior end of the body, the last two segments (cauda) are variously modified to inclose the sexual organs of the adult flies.

The head

The head is usually small and flattened, occupying the anterior ventral part of the body. The eyes differ in size in the various groups, in some (Erioptera, Elephantomyia) being larger in the male than in the female; in the male sex they are approximated on the median line above or beneath.

The front between the eyes is usually narrowed behind, delimited by the inner margin of the compound eye, narrowed at the posterior end, and bluntly rounded or pointed at the apex. This part is described herein as the *labrum*, or *labral sheath.* It contains the fronto-clypeus and the labrum of the imago. At its tip it bears two more or less divergent lobes, these being in some cases closely approximated so as to appear as a single lobe; these are herein termed the *labial lobes* or *sheaths,* and they contain the so-called paraglossae of the adult fly.

On either side of the labral sheath, and usually divergent and lying along the posterior margin of its face, are the sheaths of the maxillary palpi, which in most cases extend beyond the knee joint of the fore legs. In almost all the Limnobiinae these are short and stout and almost straight, but in the majority of the tipuline forms they are curved at their tips, which in most species are actually recurved and offer an easy means of distinguishing members of this subfamily. In many of the Limnobiini the margins of the cheeks project as flattened ledges overlying the joint of the fore legs.

The antennae arise from above or between the eyes and bend laterad and thence caudad around the eyes, in some forms, such as Elephantomyia and the males of other species, lying across the face of the eyes. The antennae usually end just beyond the roots of the wings, but in the males of some species (Eriocera) they extend beyond the tips of the wings. The basal segments (scape) of the antennal sheath are often armed with

spines or tubercles, and very often the organ is angulated at the end of each segment of the adult antenna inside.

At its vertex, between or just dorsad of the antennal bases, the head may bear a crest which is usually bilobed and setiferous. In some species this cephalic crest is quadrituberculate, there being a smaller secondary crest behind or before the primary one. In the Tipulini the crest is very inconspicuous and but weakly setiferous. In most of the Limnobiini it is lacking or nearly so.

The head may be variously armed with spines, tubercles, or setae; in *Eriocera spinosa,* for example, there are spines or strong tubercles on the antennal scape, on the clypeal region, and even on the face of the eye. In some cases there are setae on the front between the eyes, on the clypeus, and on the cheek.

The thorax

The pronotum of the thorax is small. The ventral part is closely applied to the head and often has small setiferous tubercles close to the breathing horns. The pronotal breathing horns are variously developed in the different tribes and genera, and are discussed here in general terms only.

Many species are propneustic, the pronotal horns alone being functional. Other species (in Hexatomini and Eriopterini) are peripneustic, the second to the seventh abdominal segments being provided with functional lateral spiracles in addition to the breathing horns; other pupae have lateral abdominal spiracles, but in most cases they are merely vestigial. Some pupae are amphipneustic, there being in addition to the breathing horns a conspicuous pair of spiracles on the dorsum of the eighth abdominal segment (Rhamphidia, Ula, Epiphragma; in the typical species of Limnobia these are present but they are small and are probably nonfunctional).

In the Ptychopteridae the breathing horns are very unequally developed, one being enormously elongated and filiform while the other is abortive. In some Tipulini (Longurio, Prionocera, Tipulodina) the horns are likewise greatly elongated, but in these cases they are shorter than the body and are approximately subequal in size, or at least are not so disproportionately unequal.

In the Limnobiini the breathing horns are usually stout and broad, in the typical Limnobaria (Limnobia, Dicranomyia) being subquadrate,

subcircular, or even broader than long. In Elliptera they are earlike and very large. In Antocha a unique condition is found, in that the apparatus is divided into eight stout filaments. In the Eriopterini and the Hexatomini the horns are usually long and cylindrical or slightly flattened, and straight or but slightly curved. There are numerous deviations from type, however. In Gnophomyia and some species of Gonomyia (*alexanderi* and *kansensis*, for example), the horns are trumpet-shaped; in *Gonomyia sulphurella* they are compressed and flattened into fanlike structures. In several widely separated paludicolous genera, such as Ulomorpha, Pseudolimnophila, and Prionocera, the breathing horns are split at their tips into two conspicuous flaps with fimbriate margins, an obvious adaptation to an existence in mud. Often the breathing horns are very small (as in Elephantomyia, Teucholabis, and Trichocera) or even microscopic (Dicranoptycha). *Limnophila hyalipennis* (Zett.) is described by Beling (1886:198–199) as lacking the breathing horns, but this is presumably an error of observation which may be due to a defect in the material studied, or possibly the horns are sessile or reduced as in Dicranoptycha. In some species (Erioptera, Eriocera) the horns are stout at the base but taper rapidly to the acute points. In many Pediciini the tips of the horns are expanded and usually obliquely truncated, with a row of breathing pores around the margin. The tipuline breathing horns are remarkably uniform in general structure, being usually elongated cylindrical in shape, of moderate length, and with the tips slightly expanded. The most conspicuous deviations from type are the short, flattened, and somewhat clavate horns of Tanyptera.

The thoracic mesonotum is very convex, or gibbous in many species (Limnobiini and some Hexatomini). In other species it is declivitous, with a high transverse crest (Eriopterini). This crest may be armed with numerous small spines (Helobia); from two to four powerful hooks (Molophilus, some species of Ormosia, some species of Erioptera, Teucholabis); from six to eight tubercles set with stiff bristles (Gonomyia); or abundant small setiferous tubercles on either side of the median line, these being less conspicuous along the shoulder (most species of Ormosia and of Erioptera). In *Eriocera longicornis* there is a median spine or tubercle on the scutellum. In some Cylindrotominae the metanotum bears spines. The extreme lateral or ventral margin is produced into a blunt or somewhat pointed angle just above the wing

root; this is usually armed with from one to three setae. Various other setae usually occur on the mesonotum.

The leg sheaths lie along the ventral side of the pupa. There is, in the various groups, a considerable difference in the length of the sheaths, their position, and the relative arrangement of the ends of the tarsal segments. In the Bittacomorphinae, the fore legs overlie the middle legs. In the Rhyphidae the fore legs overlie the middle pair, which, in turn, overlie the hind legs. In the Ptychopterinae and in the Tipulidae, all three pairs of sheaths lie parallel along the midventral area, those of the hind legs being outermost along the wing sheaths, and those of the fore legs being on the inside and contiguous. In Gnophomyia the leg sheaths are very short, extending but little beyond the wing tips and reaching only the end of the second abdominal segment. In other crane-flies they are longer, in some species reaching the end of the fifth abdominal segment. Very often the tips of the tarsi are on a level. In the Limnobiini the hind tarsi are usually a little shorter, and the fore tarsi are a little longer, so that the ends of the sheaths form a blunt V. In the Eriopterini the middle legs are usually (except in Gnophomyia) much shorter than the other legs; in Helobia, moreover, the hind legs are conspicuously longer than the fore legs, so that all three sets end at different levels. A somewhat similar and parallel development is found in the tipuline forms.

The wing sheaths are moderately broad, usually ending opposite or a little beyond the apex of the second abdominal segment. The venation of the various species often shows clearly and with little distortion on the wing pad, and in such cases it is of very great help in locating certain genera. Species with a heavy pattern in the adult wings, such as those of the genera Discobola and Epiphragma, show this pattern on the wing pad in the older pupae, and this helps to confirm their identity.

The abdomen

The abdomen consists of apparently nine segments, the last two being closely approximated or fused to form the cauda. The segments are usually plainly divided into a broad dorsal (tergal) and ventral (sternal) region, and a much narrower and more restricted lateral (pleural) area. The segments beyond the first are variously subdivided into rings, or annuli, by false constrictions, there being usually one, but in some cases

two or more, basal rings and a much broader posterior ring. The segments are variously armed with setae, or spines. In the Limnobiini and some Hexatomini these occur on the basal annulus, and consist of a transverse welt which is margined (as in Antocha and Elliptera) or covered with abundant microscopic chitinized points. In some Pediciini the setae occupy both the basal and the posterior rings of the intermediate abdominal segments. In the Eriopterini and most Hexatomini, as well as in the tipuline forms, the setae occur on the posterior ring, just before the caudal margin, and consist of a single transverse row of small spines. In the Cylindrotominae the segments are often armed with prominent elongate body projections (Liogma, Triogma). In Phalacrocera elongate lobes are confined to the posterior segments of the abdomen. In the Ptychopteridae the segments are densely covered with transverse rows of long tubercles which are replaced by chitinized plates near the posterior margin of the segments. In Bittacomorpha these tubercles are stellate at their tips.

The dorsum of the cauda in most crane-flies is armed with four, five, or six conspicuous lobes which are often spinous at or near their tips. These represent the lobes that surround the spiracular disk of the larva, and their number generally corresponds to the larval condition. Thus, in the Ptychopteridae there is a single lobe, in the Pediciini there are two, and in the Hexatomini and the Eriopterini there are four or five. In the Tipulinae there are often but four evident lobes, the dorsal pair of the larva not being represented. In some generalized groups, as the Limnobaria, the Rhamphidaria, and others as indicated elsewhere in this paper, the larval spiracles persist in a more or less functional condition.

Abdominal spiracles.— In the Eriopterini and the Hexatomini there is a distinct and apparently functional spiracle on each pleurite of the second to the seventh abdominal segments, located near the base of the posterior ring. In the Eriopterini these spiracles are small and, in the cast pupal skin, appear tubular or elongate. Smaller vestigial spiracles are evident in most genera of the Tipulidae.

As has been mentioned earlier in this paper, in certain primitive genera of Tipulidae — such as Rhamphidia, Ula, Epiphragma, and to a lesser extent those of Limnobaria — there is a pair of rather large spiracles on the dorsum of the eighth segment. In *Dactylolabis cubitalis* the lateral

abdominal spiracles are protuberant, notably the pair on the second segment.

The genitalia.— The genital sheaths conceal the adult organs within. In the male the valves are usually subequal or the sternal valves are a little the longer. In the female the sheaths, or acidothecae, of the ovipositor usually have the dorsal valves considerably longer than the sternal valves and distinctly upturned at their tips. In the few groups with fleshy ovipositors, the female cauda is very difficult to distinguish from the cauda of the male. The valves are variously armed with spines or lobes, at or before the tips.

INTERNAL MORPHOLOGY

The internal morphology and anatomy of the crane-fly larva are here considered in general terms only. The two genera that have been studied in greatest detail by the writer are Eriocera and Antocha. The most important literature on the various systems of the body is cited in order to make reference to it more easily available.

The digestive system

The most important literature on the digestive system is as follows:

Ptychoptera. Grobben, 1876; Van Gehuchten, 1890.
Chionea. Brauer, Egger, and Frauenfeld, 1854:613–614, pl. 11, fig. 4.
Dicranota. Miall, 1893:242–245.
Phalacrocera. Miall and Shelford, 1897:347–351; Bengtsson, 1897.
Ctenophora. Anthon, 1908:546–551, figs. 12–35.
Holorusia. Kellogg, 1901 a; Comstock and Kellogg, 1904:56–57.

Herbivorous larvae (*Tipula, Holorusia, Ctenophora, Phalacrocera*)

In the larva of herbivorous species the alimentary canal extends the length of the body as an almost straight tube inclosed by the coiled, perforated sheets of adipose tissue. The esophagus is slender, opening into the hypopharynx. The proventriculus has a large esophageal invagination at its anterior end. The ventriculus has at its anterior end four elongated ventricular caeca, these being of two distinct lengths in pairs (didynamous) in Ctenophora, and all four alike in Holorusia. In Ctenophora there are four small, pocket-like gastric caeca near the posterior end of the ventriculus, which are not mentioned as occurring in Holorusia. At the juncture of the ventriculus and the small intestine are the four

coiled malpighian tubules. Behind the ventriculus lies the small intestine, with a caliber much smaller than that of the ventriculus. At the union of the large and the small intestine is a prominent diverticulum of very large size (in Ctenophora three times as large as in Holorusia). The large intestine gradually dilates behind to form the rectum.

Phalacrocera has the ventriculus without caeca and the hind intestine without a diverticulum, altho it is decidedly a herbivorous genus. The condition in Chionea is almost the same. In Phalacrocera, and probably in most other larvae, a peritrophic membrane (a secretion of the epithelium which incases the food and keeps it from direct contact with the epithelium) is present.

There are four malpighian tubules in all the Tipulidae that have been thoroly studied (Chionea, Eriocera, Dicranota, Phalacrocera, Ctenophora, Holorusia, Tipula, and a few others). In the Rhyphidae, likewise, there are four tubules in both the larval and adult stages. In the Ptychopteridae, however, there are five tubules, as in the Culicidae, the Psychodidae, and related families. This might indicate some basis for placing the Ptychopteridae in close proximity to the Culicidae, as has been done by Lameere (1906).

The salivary glands consist of two large coiled tubules which pass into a collecting duct and unite to form the common collecting duct that opens at the base of the hypopharynx.

Carnivorous larvae (*Dicranota, Eriocera*)

The alimentary canal in the carnivorous type of crane-flies is a short, straight tube, with a minimum of appendages such as caeca and diverticula. In Eriocera the esophagus is very long, and the ventriculus is short and without caeca. The malpighian tubules are yellow at their origin, soon passing into an orange-brown color. The intestine is short and straight, without a diverticulum.

The salivary glands in the newly killed larva of *Eriocera spinosa* are very conspicuous by their opalescent color, which persists for a day or more after death. These glands consist of two elongate-oval or cylindrical glands, of the opalescent color just mentioned. From the anterior end of each of these glands passes the long, slender, salivary collecting duct, which unites with its fellow to form a common duct opening at the mouth cavity. From the caudal end of each gland is a flattened, almost hyaline,

elongate lobe which is indistinctly pseudo-segmented, in its posterior part being in intimate connection with the abundant fat tissue.

Respiration and circulation

The most important literature on the respiratory and circulatory organs is as follows:

Ptychoptera. Grobben, 1876.
Dicranota. Miall, 1893:245–248.
Phalacrocera. Miall and Shelford, 1897:351–356.
Liogma. Müggenberg, 1901.
Ctenophora. Anthon, 1908:551–554.
Holorusia. Kellogg, 1901 a; Comstock and Kellogg, 1904:57–58, 60.
Tipula maxima. Brown, 1910.
Tipulinae, Hexatomini (especially *Tipula paludosa* and *Limnophila punctáta*). Gerbig, 1913.
General articles. De Meijere, 1895; Viallanes, 1880.

The most important works on the structure of the tracheal system with special reference to the mechanics of the spiracles, are those by Müggenberg (1901), De Meijere (1895, 1902, 1916), Brown (1910), and Gerbig (1913). Miall and Shelford (1897:351–356) discuss in much detail the structure of the heart in Phalacrocera.

In *Eriocera spinosa*, which may be considered as typical for this group of crane-flies, there are two principal tracheal trunks which lie in a dorsal position and run almost the length of the body. They are connected across by a very delicate, unbranched, simple, tracheal commissure, and send off branches laterally to supply the various organs of the body. Near the posterior end of the body they are approximated, and just in front of the spiracles they expand into the tracheal chamber. Directly cephalad of this chamber the first lateral branch passes off, numbering from the posterior end forward. Branches 2 to 8 are large and much forked. Just after leaving the main tracheal trunks, each of these sends off a ventral branch which supplies the alimentary canal and the fat tissue. Branch 3 supplies the region of the malpighian tubules; branch 4, the posterior part of the stomach; branch 5, the anterior part of the stomach; branches 6 to 8, the esophageal region — branch 6 supplying the proventriculus, branch 7 and part of branch 8 the esophagus, and the remainder of branch 8 the pharyngeal region.

The main part of each lateral branch continues laterad, at its first (anterior) fork sending a branch forward to the next branch, so as to

form a complete but much-branched lateral trachea. The branches are very diffuse and abundant and the skin is well supplied. As already stated, the cross-commissures are very delicate and are unbranched or nearly so, the dorsal regions of the body being supplied by branches from the lateral supply.

The condition of the tracheae in Antocha, the only apneustic crane-fly larva among the species here considered, may be outlined as follows:

The usual two principal trunks are present, joined across on each segment by delicate cross-commissures which send off two approximated branches except on the eighth segment. Laterad and ventrad of the principal trunks are the delicate lateral tracheae. These are joined to the main trunks by fine branches inserted about midway between the dorsal commissures, toward the posterior end of the body lying nearer the posterior commissure than the anterior one.

At the ninth segment each trunk sends off a branch from its proximal side, these branches being connected by a long commissure and supplying the posterior pair of gills. The commissure is about as long as that part of the branch between it and the trunk. Immediately caudad of, or just at, the fork, but on the ventral side, a subequal branch passes into the anterior gills; at the same point the delicate lateral tracheal trunk finally ends in the main trunk. Caudad of this triple forking the main trunk gradually widens out into a cylindrical structure which is truncated apically, at the tip passing out into two small elongate branches, near the base with about three delicate branches, two being dorsal in position and one more lateral. All of these tracheae, to the gills and to the caudal lobes, send off many branched capillaries at frequent intervals, and the caudal lobes unquestionably function as tracheal gills.

A comparison of Antocha with Dicranota as described and figured by Miall (1893:245–248) shows, in the latter, distinct spiracles and the gills similar but much smaller. The tracheal arrangement differs in that a single branch on either side supplies both gills of that side, while the caudal lobes are tracheated by a branch that leaves the main trunk close to the spiracles. (Plate XII, 2 and 3.)

The arrangement of the tracheae at the base of the wing pad is described and figured for Bittacomorpha by Dr. Chapman in Comstock's *The Wings of Insects* (1918:36–37).

The nervous system

The most important literature on the nervous system is as follows:

Ptychoptera. Grobben, 1876.
Dicranota. Miall, 1893: 241.
Phalacrocera. Miall and Shelford, 1897: 356; Bengtsson, 1897.
Ctenophora. Anthon, 1908: 556–557.
Holorusia. Comstock and Kellogg, 1904: 58–59.

In Holorusia the brain, or supra-esophageal ganglion, is composed of two principal lobes united posteriorly and lying above the esophagus. Beneath the brain and on the under side of the esophagus lies the subesophageal ganglion, which is connected with the anterior end of the brain lobe by the circum-esophageal commissures. The above-named organs form a complete ring, or collar, around the alimentary canal. The ventral nervous system leads backward from the subesophageal ganglion on the ventral surface of the body wall. In the thorax there are four closely approximated ganglia representing the thoracic and the first abdominal segments. Beyond these and located in the abdomen are six abdominal ganglia. The ganglia send off four large nerve trunks.

The condition is similar in Ctenophora and in Tipula, there being seven abdominal ganglia, of which the first is located in the thorax and the last six in the abdomen. In Phalacrocera there are eight abdominal ganglia, the first being usually found in the first abdominal segment and the eighth in segment 10. The head ganglia are all independent of one another, not fused into a complex. The longitudinal commissures between the first five ventral ganglia are double, and those between the eight abdominal ganglia are simple (Bengtsson). In Dicranota there are likewise eight abdominal ganglia, the first being located in the first abdominal segment and the others in segments 5 to 10, there being two close together in the tenth segment.

The reproductive system

The most important literature on the reproductive system is as follows:

Ptychoptera. Grobben, 1876.
Dicranota. Miall, 1893: 248.
Phalacrocera. Miall and Shelford, 1897: 356–357.
Holorusia. Comstock and Kellogg, 1904: 58.

The reproductive organs appear early in the larval development. In Dicranota the testes lie in the ninth segment and form elongate capsules,

when sufficiently advanced giving off the vasa deferentia from the inner side of the hinder end. Even in larvae not fully matured, Miall found ripe spermatazoa mixed with spermatoblasts. No division of the testes into follicles is apparent. In Phalacrocera, also, ripe spermatazoa may be found in the older larvae.

In Phalacrocera the ovaries form a pair of cylindrical bodies tapering to each end, lying on either side of the beginning of the intestine. The ovaries are very peculiar in structure, seeming to be adapted to the almost simultaneous discharge of all the eggs.

The muscular system

The most important literature on the muscular system is as follows:

Body musculation

Ptychoptera. Grobben, 1876.
Dicranota. Miall, 1893:241.
Ctenophora. Anthon, 1908:545.
Holorusia. Comstock and Kellogg, 1904:59–60.

Musculation of the mouth parts

Phalacrocera. Bengtsson, 1897.

The fat bodies, or adipose tissue

The most important literature on the adipose tissue is as follows:

Dicranota. Miall, 1893:241–242.
Ctenophora. Anthon, 1908:554.
Holorusia. Comstock and Kellogg, 1904:56.

The imaginal disks, or histoblasts

The most important literature on the imaginal disks is as follows:

Phalacrocera. Miall and Shelford, 1897:357–358.
Ctenophora. Anthon, 1908:555.
Holorusia. Kellogg, 1901 b; Comstock and Kellogg, 1904:61.

PHYLOGENY

The origin and phylogenetic development of the various groups of crane-flies is still largely problematical. The evidence supplied by the adult flies of the most generalized living groups points to an ancestor which in many respects resembled the recent Mecoptera, or scorpion

flies. That this resemblance is presumably not fundamental is suggested by the immature stages of these same generalized forms, which show but few features that can be reconciled with those of a panorpid-like ancestor. Unfortunately the fossil record helps but little. At the beginning of the Tertiaries, crane-flies were already numerous both in species and in individuals, but in most cases they are clearly referable to existing genera. It is evident, then, that the investigator must go still further back for his evidence, and the fossil crane-flies of the Upper Mesozoic are, unfortunately, still largely unavailable. The phylogenetic development of the group may be considered from two standpoints, the geological record and comparative morphology.

THE GEOLOGICAL RECORD

The most important works on fossil crane-flies are those of Loew (1850), Scudder (1894), Handlirsch (1906–08, and 1910, a and b), Meunier (1906), and Cockerell (1910, 1913, 1916, and 1917, a and b). The writer is indebted to Professor Cockerell for assistance in determining the age of many of the fossil-bearing beds. Excellent accounts of the various deposits may be found in Cockerell (1913) and in Tillyard (1917).

The Tipuloidea, representing the superfamily of crane-flies, is herein considered as being constituted of six families, of which two, the Eoptychopteridae and the Architipulidae, did not survive the Mesozoic period. The Eoptychopteridae are known only from the Mecklenburg Lias (lowest Jurassic), and include but three monotypic genera. The Architipulidae are known from the same formation and include eight species arranged in three genera. The other four families contain recent forms and are included in this paper.

The North American Eocene and Miocene, as represented by the White River and Green River beds and the Florissant shales, respectively, give evidence of having had a northern fauna, especially in the Eocene. This is well shown by the great development of the Cylindrotominae, which in the White River basin almost dominated the crane-fly fauna during the Eocene. It seems probable, moreover, that the group was forced into colder regions of the globe during the Oligocene, when the tropical element reached far to the north. No group of crane-flies that can be considered as being tropical has yet been found in the Florissant. On the other hand, the European Oligocene, as shown by the Gurnet Bay beds

and the lower Oligocene Baltic amber, has a considerable tropical element apparent — as, for instance, Styringomyia, found in both formations, and Trentepohlia, Polymera, and Brachypremna, the last two being amber records. In connection with these two last-named genera, as fossils known only from the Baltic amber, it should be noted that each is found living to-day only in America, where they are confined to the austral and tropical regions.

The Tanyderidae are represented by the Oligocene Macrochile (amber) and Etoptychoptera. At present this is still a very small group, including but two genera and nine species.

The Ptychopteridae include a Ptychoptera from the Bohemian Krottensee (probably upper Oligocene) and a Bittacomorpha from the Florissant.

The Rhyphidae (Trichocerinae) are represented by two species from the Baltic amber and one or two additional species from the Miocene.

The Tipulidae may be considered in general terms only. But one tipulid is listed by Handlirsch as being known from the Mesozoic. In the earliest Tertiaries, however, a variety of species is found in this family which almost parallels their recent development.

The Limnobiini first appeared in the Eocene (Dicranomyia, Geranomyia). In the lower Oligocene, numerous species of Dicranomyia and Rhipidia occurred. In the Miocene, Dicranomyia was common, tho probably not so rich in species as at present. Rhamphidia is found in amber, and Antocha has been described from the Florissant Miocene by Scudder; the latter record, however, seems very doubtful to the writer, judging from Scudder's figure and description.

The Hexatomini are represented by Ula, Limnophila, Eriocera, and Polymera in amber, and by Limnophila in the Florissant shales.

There is no record of the Pediciini being preserved as fossils.

The Eriopterini are well represented in the Baltic amber by Erioptera, Gnophomyia, Gonomyia, and related genera, and also in the Miocene by Gonomyia, Cladura, and others. Toxorhina, an apparent relative of Elephantomyia, occurs in the Baltic amber.

The Styringomyiini are represented by the only living genus, Styringomyia, a fly of uncertain affinities, in the Gurnet Bay Oligocene (Cockerell, 1917c and 1919) and in amber, reappearing in the Pleistocene African copal.

The dominance of the Cylindrotominae (genus Cyttaromyia) in the Eocene and Miocene of the North American fauna has already been mentioned. No records of this group from the European Oligocene are available. The recent species of the subfamily are practically all forms belonging to cold, temperate regions, the few Oriental species of Stibadocera coming from mountains at considerable altitudes.

The Tipulinae have been found as far back as the Mesozoic, but the records are not entirely satisfactory. In the lowermost Tertiaries, however, undoubted tipuline forms occur. Species occur in the Green River shales of Colorado (Eocene). The group was well represented in the Oligocene (Baltic amber, Tulameen beds of British Columbia, Krottensee, and Gurnet Bay), and was very common in the Miocene (Radoboj, and especially in the Florissant of Colorado, where some twenty-five species of Tipula and closely allied genera or subgenera have been described by Scudder and Cockerell).

Tipulidae of the Pleistocene are not numerous, only a few having been made known from the refuse of lake dwellings in England (Dicaera, apparently related to Ctenophora), and in the African copal, including such genera as Styringomyia, Elephantomyia, and Toxorhina.

COMPARATIVE MORPHOLOGY

The morphology of the various stages of crane-flies has been detailed elsewhere in this paper and need not be repeated here.

PHYLOGENETIC CONSIDERATIONS

The eucephalous familes of crane-flies are undoubtedly lower, phylogenetically, than the Tipulidae, and the latter have been derived from the former. The generalized type recurs in all three subfamilies of the Tipulidae, and it is uncertain which of these three should be placed lowermost. Presumably all three groups arose from an immediate common ancestor, or the Tipulinae and the Limnobiinae arose from one point of the tree, the Cylindrotominae developing from the limnobiine stem at a somewhat later period. The accompanying phylogenetic tree (Plate XII, 4) graphically illustrates this apparent evolution of the group. The Limnobiini show but little deviation from the fundamental type. From the level of the lowermost Hexatomini (Ula and Epiphragma), in close proximity to the Limnobiini, the remaining groups of crane-flies can be

derived — the Pediciini and the Eriopterini on the one hand, the hexatomine divisions on the other. The highest levels of development of their respective types are apparently Diotrepha (Limnobiini), Dicranota (Pediciini), Gonomyia (Eriopterini), and Hexatoma (Hexatomini).

The immature stages of the Tipulidae of the antipodal regions (Australia and Chile) are entirely unknown, and their discovery may bring to light striking novelties that may well upset the present ideas of classification. The largest remaining gaps in the present knowledge of the Nearctic fauna relate to the genera Atarba, Toxorhina, Cryptolabis, Phyllolabis, and Megistocera, but it is not expected that any major groups will have to be created for their reception.

LIFE HISTORIES OF CRANE-FLIES, WITH KEYS AND DESCRIPTIONS OF THE SPECIES

Various classifications and arrangements of Diptera have been proposed in the past, and the principal evolutionary changes in the entomologist's conception of classification are herein indicated.

The groupings in the superfamily Tipuloidea have been very diverse. Brauer (1883) separated the eucephalous families from the Tipulidae (Polyneura). Osten Sacken (1893) placed the Tipulidae in the *Nemocera vera*, the Rhyphidae in the *Nemocera anomala*. Coquillett (in Howard, 1912:85–86) included the Tipulidae in his superfamily Tipuloidea, but separated the Rhyphidae, placing the latter in Bibionoidea. Lameere (1906) gave a classification that had little basis in fact, the Rhyphidae being considered by him as Brachycera and the Ptychopteridae being placed with the Culicidae. Knab (1915), working on the respiratory systems of the larvae, demonstrated the hitherto unnatural groupings of the families of the Nemocera, and arranged the crane-fly families, along with a few others, in the group Polyneura, a group coordinate in rank with the previous conception of the Nematocera. The latest grouping, that of Malloch (1915–17 b), was based on a broad knowledge of both the adult flies and the immature stages; and here, for the first time, one gets the true conception of the superfamily limits — the inclusion of the Ptychopteridae, the Tipulidae, and the Rhyphidae in a single major group. Malloch's arrangement is herein adopted, with the following exceptions: (1) the Limnobiidae are not held as constituting a separate family, but are united with the Tipulidae; (2) the family Tanyderidae has been

erected, to include the generalized Tanyderina which have hitherto been placed with the Ptychopteridae.

The immature stages of the four families of the Tipuloidea are readily separable. The larvae of the Tipulidae can be confused only with those of certain low brachycerous forms, as, for example, the Leptidae. In the Brachycera the mandibles work vertically and parallel to each other; in the Nematocera, including the Tipuloidea, they operate transversely or obliquely against the teeth of the mentum and the hypopharynx. The presence of fleshy lobes surrounding the spiracular disk is a character possessed by almost all Tipulidae. The larvae of a few groups of brachycerous Diptera, such as certain Leptidae, Sciomyzidae, and other families, possess entirely similar caudal lobes but are readily recognized by the small and very reduced head capsule.

The eucephalous families of the Tipuloidea may be distinguished by means of the characters indicated in the following keys:

Larvae

1. Body eucephalous, head non-retractile; amphipneustic or metapneustic..............2
   Head incomplete behind, retractile; not amphipneustic..............TIPULIDAE (p. 791)
2. Caudal end of body prolonged into a slender breathing tube; metapneustic..........3
   Caudal end of body not prolonged into a breathing tube; amphipneustic. RHYPHIDAE (p. 787)
3. Breathing tube stouter, non-retractile; gills large, pinnately branched; punctures of head multisetose; found in wet decaying wood..............TANYDERIDAE, supp. (p. 769)
   Breathing tube slender, completely or partly retractile; gills slender, cylindrical, unbranched; punctures of head with simple or plumose hairs; found in wet earth. PTYCHOPTERIDAE (p. 772)

Pupae

1. One of the pronotal breathing horns greatly elongated, much longer than the body, the other breathing horn very short, abortive. (Family PTYCHOPTERIDAE, p. 772)......2
   Breathing horns short, or, if elongated (some Tipulinae), not longer than the body and the difference in size not so apparent..3
2. Tarsal sheaths lying side by side, parallel......................**Ptychopterinae** (p. 773)
   The fore tarsal sheaths overlying the middle pair, the four middle and hind tarsi the longest, parallel..**Bittacomorphinae** (p. 779)
3. Tarsal sheaths overlying one another in pairs.....................RHYPHIDAE (p. 787)
   Tarsal sheaths lying side by side.................................TIPULIDAE (p. 791)

The pupae of the Tanyderidae are still unknown.

It is possible that Bittacomorphella (page 779) has short breathing horns; in this case this genus would run down to couplet 3 above, but by the arrangement of the tarsal sheaths it runs out as indicated in couplet 2.

FAMILY **Tanyderidae**

Larva (supposition).— Body eucephalous, metapneustic. Integument smooth, shiny white. Last two segments of abdomen produced into a stout, non-retractile breathing tube, which is distinctly five-lobed at the tip. Tracheal gills two, very large, pinnately branched. Head with scattered punctures, which are multisetose; lateral plates of head united across venter. Mandibles opposed, narrow, tridentate. Maxilla with palpus two-segmented, the outer lobe digitiform, pubescent. Labrum small, semi-circular, with two punctures; clypeus with four punctures.

Pupa.— Unknown.

The Tanyderidae comprise a group of primitive crane-flies including but three recent genera, with ten species. Of these the genus herein considered, Protoplasa, with three known species, is found in the Northern Hemisphere. All that is known concerning the biology of supposed species of this group pertains to *Protoplasa fitchii* and is discussed below.

Genus **Protoplasa** Osten Sacken (Gr. *first* + *to form*)

1859 *Protoplasa* O. S. Proc. Acad. Nat. Sci. Phila., p. 252.
1878 *Idioplasta* O. S. Cat. Dipt. N. Amer., p. 222.

The genus Protoplasa is confined to temperate North America. There are three known species, of which *P. vipio* O. S. and *P. vanduzeei* Alex. are western in their distribution, while *P. fitchii* O. S. is eastern. The general characters of the supposed larva are given above; the detailed account in connection with the species *P. fitchii* follows.

Protoplasa fitchii O. S.

1859 *Protoplasa fitchii* O. S. Proc. Acad. Nat. Sci. Phila., p. 252.

The remarkable insect *Protoplasa fitchii* is one of the rarest of the local crane-flies. There are scarcely a score of specimens extant in the various collections of the country, most of which are from the mountainous section of North Carolina. The fly has not been reared, but the writer has in his possession a larva that he refers with much confidence to this species. It is one of the most remarkable dipterous larvae that have ever come to the writer's notice, and, whether or not it belongs to Protoplasa, it should certainly be called to the attention of entomologists in the hope that it may some day be bred and its identity confirmed or ascertained. These peculiar dipterous larvae were discovered by H. S. Barber, C. T. Greene, and

R. C. Shannon, on the Potomac River near the mouth of Dead Run, Fairfax County, Virginia. They were found during the latter part of May, 1916, in a much-decayed maple log, where they were associated with the larvae of the syrphid fly, *Temnostoma bombylans* (Fabr.) (Barber, 1913). Greene attempted to rear the larvae procured at this time, but did not succeed. In May, 1917, he sent the writer one of the preserved larvae for study. Later Dr. Viereck was interested in the matter, and on May 27 he procured one fine, healthy larva, which was sent to the writer at Ithaca, New York. It arrived safely on the 29th, and was at once placed in rearing. Unfortunately this larva died the day after it came into the writer's possession, and this remarkable insect still remains unreared. Associated with this larva in the pieces of decaying maple in which it was shipped, were larvae of Temnostoma and a larva and a pupa of the tipulid *Epiphragma solatrix*.

The evidences that this larva is that of Protoplasa are numerous. It belongs, without doubt, to the Nematocera, and the immature stages of all the remaining families of that division have been made known. Many features in this larva point strongly to the condition in other families of crane-flies. The eucephalous condition of the head, and the elongate breathing tube, are suggestive of the Ptychopteridae; the five-lobed spiracular disk, the anal tracheal gills, the metapneustic respiratory system, and other features, are very similar to conditions in certain Tipulidae. However, there are conditions obtaining here that are found nowhere else in the Diptera, so far as is known to the writer, such as the combination of a eucephalous head of primitive organization, a stout, non-retractile breathing tube, the large, pinnately branched anal gills, the multisetose punctures on the head, and the details of structure of the mouth parts. The multisetose punctures are suggestive of the branched or plumose hairs of Ptychoptera, and give a possible hint of the origin and ancestry of this condition in the latter group. The writer cannot but regard it as suggestive that the larvae are found in direct association with those of Epiphragma in saturated decaying wood. He has mentioned in other papers (Alexander, 1910:254, and 1919 d:883, 915) the remarkable superficial resemblance that exists between the adult flies of *Epiphragma fascipennis* and those of Protoplasa, both forms having very handsomely banded wings of a pattern not found in other species in the local fauna.

The only observations on the adult flies that the writer has ever been able to make were in reference to five specimens taken in New York State in 1909 (Alexander, 1910:254). These were swept from rich vegetation along the banks of the Sacandaga River in northeastern New York. The adult flies have never been recorded from the vicinity of Washington, but are regional, since the species ranges thruout the eastern United States as far south as Georgia (in the mountains).

Larva.—Total length, 11.8 mm.
Length excluding breathing tube, 5.6–6 mm.
Length of breathing tube alone, 5.8–6.2 mm.
Length of ninth segment of abdomen (chitinized part of breathing tube), 3.4–3.6 mm.
Length of anal gills, 2–2.1 mm.
Diameter of body, 2.3 mm.

Coloration pure white, head and apical two-thirds of breathing tube pale brown, chitinized. In the living larva there is a transparent, subcircular area on the dorsum of segment 7 thru which the beating of the heart can be clearly seen, but in preserved specimens this area is hard to perceive. (Plate XIII, 5)

Body eucephalous, entirely smooth, shiny, dorsum of segments 2 to 9 each with a transverse group of tiny points. Thorax with the first segment longer than the succeeding two segments taken together, narrowed anteriorly, broader behind; mesothoracic segment about half as long as the first and about twice as long as the very narrow metathorax. Abdominal segments gradually increasing in length to the seventh; segments 8 and 9 abruptly narrowed into a stout, elongate breathing tube which is about equal in length to remainder of body; basal, or proximal, part of tube (segment 8) shorter than terminal part (segment 9) and not chitinized; segment 9 elongate, chitinized, with a deep transverse constriction a short distance before tip; this apical part, and the region just before the constriction, smooth, the remainder of the last segment with numerous delicate transverse wrinkles. Spiracular disk (Plate XIII, 6) surrounded by five lobes, one dorsal, two lateral, and two ventral in position; dorsal lobe the smallest, lateral lobes the broadest; lobes tipped with sharp, chitinized spines, which are continued for a short distance down the outer face of each lobe; fringes of long hairs along margins of lobes; disk with a brownish tinge around spiracles and an elongate-oval median mark between, and slightly below, the spiracular level; inner face of ventral lobes with indistinct, tiny, brown punctures. Spiracles large, separated by a distance about equal to diameter of one. Anal tracheal gills two, one on either side of the base of segment 8, very large and pinnately branched, there being about fifteen branches to each gill; each of these branches constricted into four or five lobules; lobes at their tips broadly obtuse (Plate XIII, 9).

Head short and broad, epicranium chitinized. Across ventral face, the sclerite firmly united by a narrow transverse band; median part densely punctulate, this area delimited laterally and posteriorly by an indistinct curved line. On dorsum, the prefrons conspicuous and the clypeus distinct from the labrum. Head and mouth parts provided with numerous setiferous punctures, each of which is multisetose (from five to eight setae to each puncture). Chaetotaxy of epicranium (Plate XIII, 7) with three lateral groups of long bristles, the

posterior group being the longest and most dorsal in position; on ventral face, four punctures on either side (Plate XIII, 8); prefrontal sclerite apparently lacking setae, but on the epicranium proper, along margin of prefrons, a longitudinal group of six punctures on either side, the anterior pair the longest. Labrum semicircular in outline, outer margin fringed with long, stiff hairs; dorsal surface with two transverse punctures. Clypeus narrowly transverse, with four setiferous punctures in a transverse row. Dorsal median part of epicranium forming a subquadrate lobe whose lateral angles bear brushes of hairs; laterad of these angles a rounded hollow overlapped by a flat, bilobed operculum (this may be some modification of the antennae which should occupy about this position on the head). Mandible elongate, strongly chitinized, tridentate, the apical tooth the longest and more acute than the others, the middle tooth bluntly obtuse; inner posterior angle of mandible produced proximad beneath outer lobe of maxilla into a bluntly rounded lobe; mandible with a group of curved setae on scrobe near base, and a group of longer bristles lying distad and mesad of these setae on dorsal face of mandible. Maxilla with base, in a position of rest, concealed beneath head-chitin; palpus stout, antenniform, two-segmented, the basal segment short and stout, the apical segment much shorter and narrower, with a small, lateral, sensory papilla; outer lobe of maxilla produced cephalad as a stout, digitiform lobe which is densely hairy.

FAMILY Ptychopteridae

Larva.— Body eucephalous, metapneustic, long and slender, the caudal end prolonged into a more or less completely retractile breathing tube bearing the spiracles at the tip. Lobes surrounding spiracular disk indistinct. Anal gills two, elongate-cylindrical, unbranched. Integument with tiny hairs (Ptychoptera), or with slight warty protuberances (Bittacomorpha), or with conspicuous elongate tubercles (Bittacomorphella). Pseudopods on abdominal segments 1 to 3 each bearing a curved claw. Head complete; eyespots distinct. Mandibles opposed. Mentum many-toothed (Ptychopterinae) or merely bilobed (Bittacomorphinae).

Pupa.— Usually with one of the two pronotal breathing horns greatly elongated, much longer than the body (this may not be true in Bittacomorphella); in Ptychoptera and Bittacomorpha it is the right horn that is elongated, the left being degenerated; in Bittacomorphella the right horn is degenerated. Tarsal sheaths all parallel in the Ptychopterinae, the fore pair overlying the middle pair in the Bittacomorphinae. Abdomen covered with setiferous tubercles arranged in transverse rows on tergites and sternites, and more or less in longitudinal rows on pleurites. Cauda with a powerful dorsal median lobe near base of segment 8.

The family Ptychopteridae includes three genera falling in two tribes: the Ptychopterinae including the single genus Ptychoptera, and the Bittacomorphinae including the "phantom crane-flies," Bittacomorpha and Bittacomorphella. The habits of these species are discussed below in connection with the various genera. The following keys separate the subfamilies of the Ptychopteridae:

Larvae

Mentum with outer margin finely serrated; mandibles with three large outer teeth; pseudopods small; coloration yellow or brown........................**Ptychopterinae** (p. 773)
Mentum bilobed, not toothed; mandibles with a single large outer tooth; pseudopods prominent, each with a conspicuous curved claw; coloration rusty red or black. **Bittacomorphinae** (p. 779)

Pupae

All tarsi lying parallel; wing pads with *M* branched..............**Ptychopterinae** (p. 773)
Fore tarsi lying above middle tarsi; wing pads with *M* unbranched. **Bittacomorphinae** (p. 779)

The immature stages of this group of flies have long been known, having been investigated by Réaumur (1740), Lyonet (1832), and other early workers. The immature stages of the common American species *Ptychoptera rufocincta* are herein recorded for the first time. The unknown Ptychoptera described by Malloch (1915–17b:240–241) is evidently *P. lenis* O. S. and is here considered as that species.

The most important literature on the Ptychopteridae is as follows:

Ptychoptera paludosa	Larva, pupa, general	Réaumur, 1740, pl. 6.
Ptychoptera paludosa	General	Wesenberg-Lund, 1915:348–351.
Ptychoptera lacustris	Larva	Beling, 1886:171–172.
Ptychoptera contaminata	Larva, general	Van Gehuchten, 1890. (Histology of the alimentary canal.)
Ptychoptera albimana	General	Cameron, 1917:65.
Ptychoptera albimana	Larva, pupa, general	Topsent, 1914–16.
Ptychoptera sp. (*lenis* supp.)	Larva	Malloch, 1915–17b:240–241.
Ptychoptera sp	General	Léger and Duboscq, 1909. (Protozoan parasites.)
Ptychoptera sp	Larva, general	Grobben, 1876. (Morphology.)
Ptychoptera sp	Larva, general	De Meijere, 1916:188–191, figs. 14–20. (External morphology.)
Ptychoptera sp	General	Lyonet, 1832.
Bittacomorpha clavipes	Larva, pupa, general	Hart, 1898 [1895]:189–195.
Bittacomorpha clavipes	General	Needham and Betten, 1901:574.
Bittacomorpha clavipes	General	Howard, 1912:95–96.
Bittacomorpha clavipes	Larva, pupa	Malloch, 1915–17b:239–240.
Bittacomorpha clavipes	General	Weston and Turner, 1917:53.

Van der Wulp (1857), Miall (1895), Grünberg (1910), and Brunetti (1912) also give general accounts of the immature stages of Ptychoptera, for the most part taken from the earlier works cited above.

SUBFAMILY **Ptychopterinae**

Genus **Ptychoptera** Meigen (Gr. *fold* + *wing*)

1800 *Liriope* Meig. Nouv. Class. Mouch., p. 14 (*nomen nudum*).
1803 *Ptychoptera* Meig. Illiger's Mag., vol. 2, p. 262.
1856 *Ctenoceria* Rond. Dipt. Ital. Prodr., vol. 1, p. 187.

Larva.— Head oval to subpyriform, broadest behind, narrowed in front, not heavily patterned above; setae of head branched or plumose. Submentum large, usually but a little narrowed posteriorly, the anterior lateral angles slightly produced; mentum broader than long, outer margin with numerous teeth (18–22). Prementum with palpi rather small, lying parallel, densely hairy on outer, or ventral, face. Mandible with three powerful outer teeth and about six smaller inner teeth. Maxilla with the cardines elongate-triangular, with three setiferous punctures; maxillary palpi antenniform, cylindrical. Labrum broad, transverse, with dense tufts of hair beneath. Integument almost smooth, without prominent warty elevations. Pseudopods low, with small claws.

Pupa.— Head small, with a reduced cephalic crest. Sheaths of maxillary palpi elongate, the tips projecting around knee joints of fore legs. Leg sheaths with all the tarsi parallel, not overlapping one another. Wing sheaths with media branched. Pronotal breathing horns very unequal, one (usually the right) exceedingly elongate, longer than remainder of body, the other tiny, degenerate. Abdomen set with transverse and longitudinal rows of small setiferous tubercles on the segments.

Ptychoptera is a small genus including sixteen described species, almost all occurring in the Holarctic region, with a few species in India and Formosa. Two species are found in tropical Africa, and another, an undescribed form, in southern South America; hence the genus is probably found thruout the world in countries in the temperate zones, with the probable exception of Australia.

The literature on the immature stages of this genus is summarized under the family account.

Topsent (1914–16) has furnished the best account of any species of the genus Ptychoptera. His observations refer to *Ptychoptera albimana.* The following notes are extracted from Topsent's paper:

> The eggs range in number from 520 to 587, averaging 554. They are pale yellow, slightly arcuated, the surface curiously ornamented, the dimensions being 0.825 by 0.264 millimeters. The duration of the egg stage is seven days. The newly hatched larva measures 3.85 millimeters, the respiratory tube 0.99 millimeters. The adult larva measures 77 millimeters, of which the respiratory tube is 20 millimeters. The growth of the larva is rapid. When fifteen days old it measures, when extended, 25 millimeters. When sixty-seven days old, it measures 45 millimeters. The pupal stage is from ten to twelve days, averaging eleven days. There are normally two generations a year.

De Meijere (1916:188–191) gives a critical account of the structure of the larva of a European Ptychoptera. It agrees well with the description of *P. rufocincta* given below, the most conspicuous differences shown by De Meijere's species being as follows: labium with the submentum having the sides straighter; mentum with the anterior margin evenly, but gently, convex, with only eighteen evident teeth. The details of the maxilla,

especially of the setae on the cardines, are not the same. However, the generic characters given above include all the species to which the writer has been able to refer.

Malloch (1915–17 b: 240–241) describes and figures an American Ptychoptera which is presumably *P. lenis* O. S. It agrees closely with the other forms in most respects. The author indicates the mentum as having three distinct parts, the median part being projected beyond the level of the lateral parts and having more teeth (eight instead of six). Malloch's specimens were taken in the Yellowstone Park, Wyoming, in August, 1890. From the locality data it is almost certain that the larvae belong to the common *Ptychoptera lenis* of the western United States.

Tonnoir (1919) describes a curious sexual dimorphism in the genus Ptychoptera.

Ptychoptera rufocincta O. S.

1859 *Ptychoptera rufocincta* O. S. Proc. Acad. Nat. Sci. Phila., p. 252.

The species *Ptychoptera rufocincta* is common around wet swales and among open shrubbery. The adult flies are on the wing from May to early July, and again in late August and early September; they may be double-brooded. In appearance they are conspicuously unlike their relatives of the Bittacomorphinae, rather resembling certain large fungus gnats (Mycetophilidae).

The larvae live in situations similar to those frequented by Bittacomorpha, and often occur in the same associations — with larvae of *Limnophila (Lasiomastix) macrocera*, *Pilaria tenuipes*, *P. recondita*, and *Erioptera chlorophylla*, as well as with many Chironomidae, leeches, nematode worms, and mollusks. In appearance they are strikingly different from the larvae of Bittacomorpha, being pale, white or yellowish white, with the body almost smooth, not covered with the dense transverse rows of setiferous tubercles found in Bittacomorpha, and with the pseudopods on the basal abdominal segments poorly developed. The larvae of this species are smaller than those of Bittacomorpha, with the head proportionately much smaller. In structural details, however, they are rather similar to the larvae of Bittacomorpha. The larvae of *Ptychoptera rufocincta* feed on the decaying vegetable matter in their haunts. When fully grown, the pupa forms within the last larval skin, and the elongate pupal spiracle is coiled about the mesothorax, as described

for *Bittacomorpha clavipes* (Hart, 1898 [1895]:191). Careful breedings of this species in 1913 at Orono, Maine, placed the indoor pupal life at four days and eighteen hours, and that in nature at probably five days — an unusually short pupal duration.

Larva.— Length, when fully grown, 30–32 mm.; when fully extended, about 35 mm. Diameter, 2–2.2 mm.

Head light reddish brown, not marked with darker spots as in Bittacomorpha; body whitish or pale yellow; tomentum short, pale; seventh and eighth segments of abdomen, and breathing tube, light brown.

Body almost smooth, sparsely clothed with short, appressed hairs arranged in indistinct transverse rows, on intermediate segments of body there being about twenty of these rows; body not at all tuberculate, as in Bittacomorpha. Prothoracic segment short, not so long as mesothorax; metathorax nearly as long as preceding two segments combined. (In older larvae that are about to pupate, the right pupal breathing horn may be seen coiled underneath the skin of the mesothorax.) First five abdominal segments swollen posteriorly into a ring that completely surrounds the segments; first three abdominal segments with low, indistinct pseudopods on either side of the median line, each with a small, recurved claw; pseudopods after first pair more widely separated than, and not so well developed as, in the Bittacomorphinae. Abdominal segments 4 and 5 more elongate, swollen posteriorly but not bearing pseudopods; segment 6 narrowed behind, with a few scattered, outspreading hairs; segment 7 narrower than preceding and telescopic within itself, at about two-fifths the length there being a transverse row of long hairs marking the limit of telescoping; when fully extended, segment 7 a little longer than segment 8; segment 8 a little narrower, and telescopic basally into segment 7. (The parts of segments 7 and 8 which are exposed in the retracted condition are brown and subchitinized, and bear scattered, outspread hairs which are most numerous near the caudal end of the exposed part and here form transverse rows; similar rows of sparse, setiferous punctures are on the dorsum of the swellings on the first five abdominal segments.) Breathing tube (segment 9) retractile into segment 8 for about one-fourth its length; when retracted, completely concealing gills. Tracheal gills two, elongate-cylindrical, situated near base of segment 9; in normal position of rest, gills usually projecting about one-half their length beyond end of segment 8. Apex of breathing tube truncated but without well-defined lobes.

Head small, proportionately much smaller than in Bittacomorpha; oval to somewhat pear-shaped; narrow anteriorly, broadened behind, near posterior margin abruptly narrowed. Prefrons broad, conspicuous. (As noted by most earlier writers on the genus Ptychoptera, the head bears numerous punctures with setae which are plumose or have a branched appearance [Plate XV, 20]. The writer has examined numerous specimens under high magnification and is inclined to believe rather that in some cases several bristles arise from a single puncture and are closely approximated basally, altho free distally, and that the plumose appearance is here merely apparent. In other cases, however, actual basal fusion has taken place. The number of free tips from a puncture varies from three to six, five and six being common numbers.) Labrum broad, transverse, on disk two large setiferous punctures bearing branched setae; on either side beneath, conspicuous tufts of long hairs, these tufts continued

obliquely proximad to near median line, where there is a median lobe densely covered with long hairs. Epipharynx small, subquadrate, margin almost transverse, with about seven blunt teeth; sides of organ with long hairs which are directed backward. Labium (Plate XIV, 12) with submentum much narrowed on basal half, sides subparallel, thence expanded so that cephalic end is about twice as wide as caudal end; anterior lateral margins produced into blunt projections; mentum (Plate XV, 17) broadly subquadrate, anterior margin nearly transverse and with from twenty to twenty-two teeth forming an irregular comb. (There is considerable variation in the shape of this comb and in the form of the individual teeth comprising it; usually the median third of the mentum is produced outward beyond the lateral parts, but this condition is not always well-marked; the individual teeth may be blunt or acute. In the specimen shown the normal condition is illustrated; the central lobe includes six teeth, and each lateral part about seven teeth, the lateral teeth being usually a little the larger; in some specimens the median lobe has the teeth very indistinct, while in others there is a conspicuous tendency for the median pair to unite into a single broad tooth.) Prementum pale basally, indistinctly covered with pale papillae; palpi lying close together, subparallel, the lateral parts with short, dense hairs, the ventral face with shorter papillae; each lobe bearing at tip a small, blunt, cylindrical knob which is slightly chitinized. Antenna (Plate XV, 18) short, almost cylindrical but slightly narrowed basally, bearing on truncate apex about five sensory papillae of various diameters, one being much the largest, two others being long and very slender; one of the papillae is bisegmented, the apical part being more slender than the basal part. (De Meijere [1916, fig. 14] shows his European Ptychoptera as having the antennae two-segmented and with the sensory papillae very different from the condition found in *P. rufocincta.*) Mandible (Plate XV, 19) strong and powerful; cutting edge subtriangular, with three large outer teeth and about six or seven small inner ones; of the larger teeth the outermost is the slenderest, the third is the largest and stoutest; small inner teeth subequal in length, the outermost stout, inwardly the teeth becoming more slender; mandible on ventral face near margin with two powerful setae, the posterior one often recurved, the anterior one directed forward. Maxilla (Plate XV, 19) with cardines roughly elongate-triangular, proximal angle acute, ventral face with three large setiferous punctures bearing several bristles of unequal length (the writer has not been able to locate setae on the middle puncture); outer edge of sclerite with a fringe of long hairs, longest at narrow inner end of segment; stipites roughly triangular, with a group of short spines at apex; palpi antenniform, stout, cylindrical, with sensory papillae at tip (one large papilla, about three of medium size, and three or four small ones); outer lobe of maxilla with a small, egg-shaped or subcylindrical, knob at its outer angle, below which the rounded lobe is densely clothed with long, pale hairs; caudad of these, along margin, a row of from six to eight powerful spines and a few long hairs.

Pupa.— Total length, 34.3–40 mm.
Length excluding breathing tube, 14.5–15.8 mm.
Length of breathing tube alone, 19.8–26 mm.
Width of body, d.-s., 1.6–1.7 mm.
Depth, d.-v., 1.7–1.8 mm.

Pronotal breathing horns reddish brown, dark brown at extreme base; thorax, wing sheaths, and leg sheaths dark brown; abdomen whitish, with small tubercles and broad

chitinized apices to segments dark brown. Pupa most readily distinguished from pupa of Bittacomorpha by the venation, the position of the tarsal sheaths, and the short, non-stellate abdominal tubercles. (Plate XIV, 13.)

Anterior cephalic crest small, deeply bilobed by a broad V-shaped notch, the rounded lobules roughened and each terminated by a single long hair. Dorsad of these, two smaller and slenderer, very widely separated, tubercles, each lying just inside antennal sheaths. Antennal bases located on ventral side of head, between eyes; antennae bent dorsad and thence caudad around knee joints of fore legs, the tips lying just outside middle tibiae; apical antennal segments showing distinctly thru sheaths. Sheaths of maxillary palpi elongate, tips curved over knee joints of fore legs. Clypeus smaller and narrower than the conspicuous labium, transversely wrinkled. Labium rectangular, each half with tips obliquely truncated. (Plate XIV, 14.)

Pronotum with lateral ventral angles almost square, each with about two small setae. Breathing horns very unequal in length; the right one greatly elongated, much longer than remainder of body, enlarged at extreme base, the outer part with numerous papillae which are more numerous and more approximated toward end of organ, these papillae lying in a single straight line which makes a long spiral around organ; left breathing horn very small and degenerate, only a little longer than sheath of maxillary palpi, curved, with about a dozen papillae which are closely crowded toward apex of organ. Mesonotum finely and transversely wrinkled, prescutum with a very acute V-shaped dorso-median mark, its apex directed backward; scutal lobes projecting, each with a few tiny hairs. Postnotum with two small tubercles at about two-thirds its length, one on either side of a pale median line. Metanotum short, sheath of halteres extending just beyond base of second abdominal segment. Wing sheaths clearly showing venation, the branched media being characteristic of the genus; wing sheaths extending almost to end of second abdominal segment. Leg sheaths with tips of fore and middle tibiae enlarged, and with inner apical angle of each produced into long points for the long tibial spurs of adult flies. Leg sheaths extending to just before end of third abdominal segment; all six legs lying side by side, not overlapping as in Bittacomorpha (Plate XV, 21).

First abdominal segment chitinized above, apical half with a few weak tubercles. Dorsum of segments 2 to 6 with posterior margins each having a chitinized band set with about twenty-five to thirty setiferous tubercles, the outermost ones being the largest; remainder of dorsum of each segment with irregular transverse rows of scattered tubercles, on narrow, interrupted, chitinized bands; usually one of the bands, at about midlength of segment, broader and more strongly chitinized than the others; these bands obliterated on posterior segments, but caudal band here very wide; about fifteen of these rows on segments 2 and 6, and from twenty to twenty-five rows on segments 3 to 5; these bands not regularly transverse, but anastomosing rather freely, not occupying more than half of abdominal surface; segment 7 with the broad caudal band only; tubercles rather short, with three or four short, irregular spines at tip, these not presenting a stellate appearance as in Bittacomorpha. Abdominal sternites similar to dorsum, tubercles lacking where leg sheaths rest against segments 2 and 3; segments 4 to 6 with transverse rows similar to those of dorsum but weaker; caudal bands on segments 4 to 7 very broad, the caudal margin with tubercles, there being about twenty tubercles on segment 4, the number gradually decreasing to seg-

ment 7, on which there are about fifteen. Abdominal pleurites with tubercles arranged in longitudinal rows, there being about six rows on each of segments 2 to 6, the rows being almost continuous for the whole length of abdomen; tubercles at caudal margin of each segment enlarged and powerful; on segment 6 the rows converging behind into a single powerful tubercle on caudal margin of segment; a similar enlarged tubercle on caudal margin of seventh segment; segment 7 and cauda narrowed. Male cauda (Plate XV, 22) with a prominent dorso-median lobe projecting directly away from the body; dorsal sheaths short, indistinctly bilobed; ventral sheaths very elongate, divergent (Plate XV, 23). Female cauda (Plate XV, 24) with the same prominent dorso-median lobe; acidotheca of ovipositor long, straight, beyond its midlength a blunt, conical tubercle directed laterad and slightly caudad; sternum (Plate XIV, 15) with ventral lobe only about half length of tergal acidothecae, caudal margin with three lobules.

Nepionotype.— Orono, Maine, June 24, 1913.
Neanotype.— With the larval type.
Paratypes.— Both larvae and pupae, June 24 to July 5, 1913.

SUBFAMILY **Bittacomorphinae**

The following keys separate the genera of the subfamily Bittacomorphinae:

Larvae

Size small (total length under 20 mm.); coloration black, breathing tube light yellow; breathing tube entirely retractile; body covered with very long projections which are incased in a black, horny substance; mandibles with an inner comb of teeth. *Bittacomorphella* Alex. (p. 779)

Size larger (total length over 40 mm.); coloration rusty red; body tapering gradually to the long, slender, partly retractile, breathing tube; body covered with transverse rows of shorter, stellate tubercles; mandibles without an inner comb of teeth. *Bittacomorpha* Westw. (p. 783)

Pupae

Size small (length, excluding breathing horn, under 12 mm.); right breathing horn small, degenerate; abdominal tubercles weak, tipped with several strong setae. *Bittacomorphella* Alex. (p. 779)

Size larger (length, excluding breathing horn, over 14 mm.); right breathing horn elongate, filiform, longer than the body; abdominal tubercles strong, elongate, crowned by a circlet of four or five spines and tipped with a setiferous papilla. . .*Bittacomorpha* Westw. (p. 783)

Genus **Bittacomorphella** Alexander (Gr. diminutive of *Bittacomorpha*)

1916 *Bittacomorphella* Alex. Proc. Acad. Nat. Sci. Phila., p. 545.

Larva.— Body short, covered with very prominent projections which are longest on lateral and caudal parts of body. Pseudopods prominent, with very large, curved claws. Breathing tube short, entirely retractile within body. Head subquadrate, the foramen ventral in position; setae of head unbranched. Mandible with an inner comb of teeth. Mentum bilobed, cephalic margin untoothed. Coloration black; breathing tube light yellow.

Pupa.— Right breathing horn very short, degenerate. Fore tarsi overlying middle tarsi. Tubercles on abdomen moderately elongated, not crowned by a circlet of spines as in Bittacomorpha, but tipped with a long seta.

The genus Bittacomorphella contains but two described species, the genotype, *B. jonesi* (Johns.), and the larger *B. sackenii* (Röder) from western America, the immature stages of which are wholly unknown. There is no published literature on the biology of this group of crane-flies.

Bittacomorphella jonesi (Johns.)

1905 *Bittacomorpha jonesi* Johns. Psyche, vol. 12, p. 75–76.

Bittacomorphella jonesi is a curious little phantom crane-fly, not uncommon in cold Canadian woods thruout the Northern States, where it is usually found near running water or springs and often in small, dark ravines or along shaded runs. The adult flies sometimes lurk beneath low, dark bridges and culverts, where they are often associated with species of Dolichopeza and Oropeza. An account of the habits of the adults of this species may be found in an earlier paper by the writer (Alexander, 1916b:545–546).

The larval habitat is very different from that of other local species of the family, which, as a rule, prefer open swamps, swales, or wet meadows. The larvae of this species live in rich organic mud in shaded woods. They were first found on the Bool hillside at Ithaca, New York, beneath decaying beech leaves in wet or damp mud which was mixed with old beechnuts, hulls, acorns, butternuts, broken decayed twigs, and similar débris. The Bool area is a very steep hillside with a general northern exposure, heavily shaded with tall forest trees. In former days it extended far to the eastward and was connected with Slim Jim Woods, near the second bridge in Forest Home. The cut area is now a pasture, but patches of skunk cabbage and cat-tails still persist. On the shaded hillside the skunk cabbage occupies pockets or level areas where the soil is largely calcareous. The forest cover consists of beech, hard maple, basswood, yellow birch, red oak, butternut, elm, a few large alders, a few aspens, and on the surrounding hillside a thick stand of hemlock. The shrubs include *Ribes floridum* L'Her., *Cornus alternifolia* Linn. f., and similar species. The herbage at this season is of the dominant skunk cabbage, young seedlings of *Impatiens biflora* Walt., *Geum rivale* Linn., and *Cardamine Douglassii* (Torr.) Britt. In places there are thick mats of mosses, *Brachythecium rutabulum* (Linn.) B. & S., on the limy soil, and Amblystegium on decaying prostrate limbs.

The curious larvae of Bittacomorphella were here found associated with the following crane-fly larvae and pupae: *Dicranomyia stulta, Limnophila adusta, L.* (*Dicranophragma*) *fuscovaria, Ulomorpha pilosella,* Penthoptera, *Molophilus hirtipennis, Erioptera megophthalma, Ormosia innocens, O. nigripila, Tipula collaris, T. oropezoides, T. cayuga,* and others. In addition numerous other natural associates were found, such as the larvae of a carabid beetle, *Nebria sahlbergi* Fisch., sow bugs, mollusks, and a great variety of other organisms. On July 10, 1914, adults of Bittacomorphella were not uncommon in the same association, at which time they were flying with other crane-flies such as *Dicranoptycha germana, Molophilus hirtipennis, M. pubipennis, Erioptera vespertina, E. venusta,* and *Gonomyia blanda.*

The first larvae of Bittacomorphella were found on May 11, and at that time were almost fully grown. They present a very remarkable appearance, being black or very dark in color and covered with numerous long projections. The breathing tube, which is capable of entire retraction within the body, is very short, and is light yellow, in contrast with the remainder of the body. The larvae are, as a rule, very slow and sluggish in their movements, but when disturbed they become more active. Large and small larvae, of two distinct sizes only, were often found in the same situations at the same time. A fully grown larva was placed in rearing on June 11, 1917, and emerged as an adult male on June 24. This provides for a pupal duration of not more than thirteen days, but the pupal stage is undoubtedly much shorter.

Larva.— Total length, 15–17 mm.
Length exclusive of breathing tube, 12.5–14 mm.
Length of breathing tube, 2.4–3 mm.; to base of gills, 1.3–1.8 mm.; beyond gills, 1.1–1.2 mm.
Greatest diameter across body, 1.7–2 mm.

Coloration dark brown to almost black, breathing tube light yellowish; in young individuals and occasional older specimens, coloration more rusty.

Body short, stout, cylindrical but appearing depressed, covered with numerous elongate projections. Breathing tube very short and capable of complete retraction within body (Plate XVI, 25). Body appearing proportionately broader, and tapering more abruptly to breathing tube, than in other species of the family herein discussed, this appearance being due to great length of lateral body projections.

The most notable single feature of larva consisting of the numerous projections from body (Plate XVII, 33), these being incased in a blackened, horny substance which is somewhat brittle. Usual shape of body extensions cylindrical, slender, and generally simple

except for those near end of body, which are asymmetrically once-forked. Basal half of projections heavily chitinized, but distal end almost transparent. Entire surface of projections beset with numerous transverse rows of short hairs, usually about nine to twelve hairs in each row, nine and ten being common, these hairs doubtless serving to hold the blackened, horny covering of the projection. Sensory papillae (Plate XVII, 34) borne at or near apices of projections, each with a long bristle; these papillae narrowed at base, thence enlarged to form a head, on which bristle is inserted; usually one or two bristles to each projection, but occasionally an additional one present, which is much smaller and degenerate. Dorsal body projections occupying transverse rows across segments, those near lateral and caudal parts of body being long and powerful, those on median region being short and degenerate; segments of thorax and abdomen subdivided into false segments, these transverse rows occupying caudal margins of these segments, there being usually from four to six of the weak projections between the powerful lateral ones. In addition to these projections, sparse branched hairs lying in the same transverse rows (Plate XVII, 35). Projections at end of body surrounding base of breathing tube all long and powerful, and, as stated above, some weakly bifurcate. Ventral body projections similar to those of dorsum but relatively smaller.

Abdominal pseudopods feebly chitinized at tips, with very large, slightly curved claws which are but little shorter than the pseudopods themselves (Plate XVII, 32). Breathing tube short and stout, surface before apex transversely wrinkled. Papillae rather numerous, bearing sense hairs scattered over surface of tube, those just back of apex short and spine-like, those farther back long and slender, very like and homologous to the bristles terminating the body projections, as discussed above. Gills two, stout, about one-third length of terminal section of breathing tube. Body projections incrusted with a black, horny substance, as discussed above; on lateral projections, apical setae likewise incased, at least basally, producing a bilobed or even a trilobed appearance; this black corneous incrustation brittle and easily removed, leaving projection and bristles intact.

Head subquadrate, sides nearly parallel, occipital foramen ventral in position (Plate XVI, 26); surface of head covered with numerous small, chitinized points which are longest on posterior angles; anterior ventral angle slightly produced; two setiferous punctures on ventral surface, one on either side just behind anterior angles, the other closer to foramen. Dorsum with setae arranged as shown in Plate XVI, 27; setae simple. Labrum (Plate XVII, 31) with four dorsal setiferous punctures along anterior margin, the median pair closely approximated; another powerful seta occupying each lateral angle on dorsal side; dense brushes of long hairs on either side beneath. Epipharynx (Plate XVII, 31) supported by two powerful chitinized arms connecting across midventral region and then extending laterad and expanding outwardly to form posterior margin of labrum; surface of epipharynx with closely appressed teeth. Labium (Plate XVI, 28) with cephalic margin of mentum almost entire, the broad median part produced cephalad and feebly bilobed; palpi with a dense fringe of long hairs around base and with sensory papillae at tips. Antenna (Plate XVI, 30) short, cylindrical, somewhat globular or barrel-shaped; about four elongate papillae and two or three shorter ones, these papillae terminal in position, the largest one occupying the inner side. Mandible (Plate XVI, 29, 30) with the outer angle a powerful hook bearing smaller teeth on ventral face at about midlength; inner angle flattened, and, besides terminal blade, bearing a comb of about five teeth, the innermost being the longest and

slenderest; a dorsal line of strong setae extending from base of outer hook inward; outer edge of mandible with two strong setae, these protected at their bases by small dorsal ears, or projections, from the mandible; dorsal face of mandible with a powerful hinged prostheca; near base of mandible on dorsal face a curious five-lobed sensory organ. Maxilla (Plate XVI, 29) with the cardo triangular, the ventral or outer face with two closely approximated setiferous punctures; stipes triangular, with three strong setae near palpus; palpus antenniform, cylindrical, rather elongated, and with about six sensory papillae at tip, one being much longer than the others; outer lobe of maxilla with cephalic margin blackened and chitinized, inner angle with a dense brush of long hairs.

Pupa.— Length excluding breathing horn, 9.5 mm.
Width, d.-s., 1.7 mm.
Depth, d.-v., 1.4 mm.

The following description is taken from the cast pupal skin of the only specimen that was reared:

Antennal bases approximated on front between eyes. Clypeus bluntly rounded at apex, transversely wrinkled. Lobes of labium (Plate XVII, 36) broad, rounded apically; maxillary palpi short and stout, broad at base, gradually narrowed to the short tip, which is not recurved. (The structure of the head and the eyes indicates some peculiar characters not possessed by the pupae of related genera, but the cast pupal skin is insufficient for accurate diagnosis.) Two bristles below eye and just above base of palpus, and a longer and more slender seta farther laterad. Sides of head behind antennae appear to be produced laterad into blunt points. Right breathing horn small, degenerate, much curved. (In the single pupal skin available, it cannot be determined whether the left horn has been broken off or is undeveloped.) Just laterad of each breathing horn a small tubercle bearing a long seta. Scutal lobes with about four stout setae. Tarsal sheaths of fore legs, as in the subfamily, overlying the middle pair but shorter (Plate XVII, 37).

Abdomen with chitinized bands extensive, as in Bittacomorpha. Arrangement of tubercles about as in other species of family. Tubercles shorter and weaker than in Bittacomorpha and not crowned by a circlet of spines, each being tipped with one or more (four or five) long setae (Plate XVII, 38); the pleural tubercles the longer and many of them multisetose. Cauda of male, in general features, similar to that in Bittacomorpha, the dorsal median lobe (Plate XVII, 39) stout, the ventral horns (Plate XVII, 40) short and powerful, directed laterad; horns on dorsal lobes apparently lacking.

Nepionotype.— Ithaca, New York, May 30, 1917.
Neanotype.— Cast pupal skin, reared June 23, 1917.
Paratypes.— Topotypic, May 15 to June 10, 1917.

Genus **Bittacomorpha** Westwood (Gr. *Bittacus* + *shape*)

1835 *Bittacomorpha* Westwood. London and Edinburgh Phil. Mag., vol. 6, p. 281.

Larva.— Form elongate, body gradually narrowed behind into the partly retractile breathing tube. Integument with transverse rows of tubercles. Pseudopods on abdominal segments 1 to 3 prominent, with large curved claws. Head subpyriform, dorsum with rows

of prominent black spots converging behind. Mandible stout, with a single powerful outer tooth. Mentum bilobed, anterior margin not comblike. Color of body, rusty red.

Pupa.— Right pronotal breathing horn very elongate; the left very small and short, subdegenerate. Fore tarsi overlying middle tarsi. Tubercles on abdomen very long, located on broad transverse bands of chitin, each tubercle with a star of four or five spines surrounding the apex, which bears a long seta.

The genus Bittacomorpha, as here restricted, includes but two species — the genotype, *B. clavipes* (Fabr.), and *B. occidentalis* Ald. of western America, concerning the biology of which nothing has been recorded. The literature on the immature stages of *Bittacomorpha clavipes* is summarized under the family account (page 773).

Bittacomorpha clavipes (Fabr.)

1781 *Tipula clavipes* Fabr. Spec. Ins., vol. 2, p. 404.
1835 *Bittacomorpha clavipes* Westw. London and Edinburgh Phil. Mag., vol. 6, p. 281.

Bittacomorpha clavipes, the "phantom crane-fly," is a common and widely distributed species thruout North America east of the Rockies. It is easily recognized by the black-and-white-banded legs, with their conspicuously enlarged and swollen metatarsi. The species is very characteristic of alder swamps and the wet margins of ponds. While in copulation the insects often fly, the female ahead, the male trailing on behind like the tail of a kite. When they alight on a plant stem, the female is invariably uppermost, the male often hanging free with none of its feet on a support. The swollen metatarsi are almost completely filled by the tracheae, and these serve to buoy the insects as they drift about in the wind. Brues (1900) describes these peculiar tracheal dilations in detail. He says, in part:

> When flying, Bittacomorpha uses the wings scarcely at all, relying in great measure upon wind currents for transportation. The legs are exceedingly light, as the exoskeleton is thin and delicate, and encloses practically no tissue which can serve to increase their weight.

In a letter from Dr. J. G. Needham, dated September 27, 1917, valuable data on this habit of drifting are furnished, as follows:

> Yesterday while crossing the Fall Creek bridge near my home on Cornell Heights, I made an observation on Bittacomorpha that interested me greatly. A breeze was blowing up the gorge, and on the breeze a Bittacomorpha was drifting rapidly upward in the usual flight attitude with broadly outspread legs, the swollen metatarsi hanging vertically, all phantom-like in slenderness and in strongly contrasting black and white. It came up from below the level of the rail, swept past within two feet of my face, and passed on upward with the breeze until lost to view, perhaps 100 feet higher than the bridge, and much farther upstream. Since

the creature can fly only very slowly and here was moving several times faster (I could not see whether it was using its wings), it was obviously drifting in the wind. Perhaps this is a normal function of the expanded metatarsi.

The larvae are usually abundant in decaying vegetable matter in rich organic mud about ponds and in swamps. The writer has found them especially numerous in the Basin Swamp at Orono, Maine (in 1913), and near Round Pond at McLean, New York. At Orono they were associated with larvae and pupae of *Ptychoptera rufocincta*, *Limnophila macrocera*, *Pilaria tenuipes*, *P. recondita*, *Erioptera chlorophylla*, a variety of chironomid larvae, numerous larvae of Trichoptera in their cases, nematodes, and leeches. Needham and Betten (1901:574–575) give a summary of the larval habitat of this species as they found it in the northern Adirondacks. Weston and Turner (1917:53) have recorded the larvae as being scavengers and thus serving as important factors in the elimination of sewage in the Coweeset Stream near Brockton, Massachusetts.

The immature stages of this interesting crane-fly have been well considered by Hart (1898 [1895]:189–195), whose account has been briefly summarized by Howard (1912:95–96). The larvae are found in shallow water that is filled with decaying vegetable matter. Here they live in the mat of dead stems of rushes, grasses, and willow leaves, in semi-stagnant or slowly flowing water. The larvae are elongate-cylindrical, with a long, partly retractile breathing tube. They are deep rusty red or brown in color, quite distinct from the pale whitish larvae of Ptychoptera or the black larvae of Bittacomorphella. They feed on decaying vegetable matter, diatoms, and mud that is filled with organic matter. They rest beneath the surface of the water, with the tip of the extended breathing tube at the surface film or just beneath the surface, in the latter case breathing by means of the small tracheal gills. When about to pupate, the very long, coiled breathing tube of the pupa is wound around the thorax beneath the larval skin. On pupation the tube soon straightens out into a very long, stiff, bristle-like structure. Like the larvae, the pupae rest beneath the surface of the water, with the tip of the breathing tube projecting above the surface film. The pupal duration is apparently about a week.

Larva.— Length when fully extended, about 60 mm.
Length of breathing tube, about 20 mm.
Diameter of body, about 2.6 to 3 mm.

Body tapering gradually at either end, posterior end prolonged into breathing tube. Usual color pale rusty brown, but the writer has found a few nearly full-grown specimens which were as pale in color as the larvae of Ptychoptera. Body covered with numerous transverse rows of small tubercles, or papillae, which bear short setae. Head broadly ovate, convex above, where it is conspicuously marked with rows of black spots, these interrupted lines converging behind. Mouth parts in general similar to those in Bittacomorphella, the main points of difference being as follows: mandible (Plate XVIII, 42) shorter and stouter, ending in a powerful outer tooth, the comb of inner teeth being reduced to about eight small tubercles, the two bristles on outer margin of mandible not overlapped by projecting " ears "; labium (Plate XVIII, 41) shorter and stouter, with a different arrangement of papillae; epipharynx long, narrowed behind, distinctly bilobed, each half with parallel rows of long, comblike teeth projecting proximad; anterior comb of epipharynx with the anterior teeth the largest, the teeth gradually reduced in size behind; posterior comb with the rows of teeth widely separated anteriorly, approximated behind so as to be contiguous or nearly so at their ends; space between these rows filled with long hairs; anterior teeth small and feebly chitinized, posterior teeth stronger. First three abdominal segments bearing conspicuous pseudopods, each terminated by a sharp, slender claw which fits into a groove on the face of the pseudopod.

Pupa.— Total length, 40–60 mm.
Length excluding breathing tube, 15.5–25 mm.
Length of breathing tube, 25–35 mm.
Degenerate breathing tube, length 2 mm., diameter 0.2 mm.
Width, d.-s., 1.8 mm.
Depth, d.-v., 2.6 mm.

Breathing tube light brown; wing sheaths brown; leg sheaths light brownish yellow and dark brownish black, alternated, corresponding to the leg markings of the adult fly. Abdomen pale yellow, rather uniformly covered with abundant brownish tubercles and transverse, chitinized plates, these brown areas scarcer on pleura and not especially abundant on apical margins of segments.

Pupa somewhat similar in general structure to pupa of Ptychoptera. Anterior cephalic crest small, lobules rounded, each tipped with a long, stout seta; immediately behind anterior crest, a similar blunt, bilobed projection of front; laterad of crest, a slender, elongate tubercle on either side, immediately behind antennal sheaths, each with a long seta; two other setiferous tubercles on head behind antennae and maxillary palpi. Antennal bases approximated between eyes. Sides of head, laterad of eyes, with a small setiferous tubercle. Maxillary palpi not recurved at tip, as in Ptychoptera, ending opposite knee joint. Clypeus elongate, gradually narrowed toward apex, transversely wrinkled; two hairs toward base near inner margin of eye. Each half of labium broad, roughly subquadrate, tips broadened and obliquely truncated (Plate XVIII, 43).

Breathing horns almost as in Ptychoptera. (Nearly always it is the right horn that is elongated, but in about ten per cent of the specimens the left horn is elongated while the right is degenerated; Hart records one specimen in which both horns were developed, but unequally, the right measuring 23 mm. and the left 13 mm.; some of the specimens recorded by Hart are larger than any that the writer has ever seen.) Wing sheaths ending almost opposite tips of fore tarsi; media unbranched. Leg sheaths (Plate XVIII, 47) with fore tarsi much shorter

than the others and lying directly over middle tarsi; tarsi of hind and middle legs parallel and extending beyond tips of fore tarsi. Scutal lobes each with about four setiferous tubercles. Thorax and first abdominal segment transversely crenulated.

Abdomen with transverse bands of chitin much broader than in Ptychoptera, so that they cover almost the entire abdominal surface; these bands with about twelve tubercles on segments 3 and 4, about ten on segment 5, and from six to eight on the posterior segments; tubercles of various sizes, small and somewhat degenerate ones being interspersed with larger ones; tubercles long and slender, each crowned by a circlet or star of from three to six (usually four or five) stout spines (Plate XVIII, 44–46), a setiferous papilla arising from the center of this circlet of spines; spines on pleura longer than those on remainder of abdomen, but not arranged in distinct longitudinal rows as in Ptychoptera, being usually more irregular, in some cases showing three or four more or less distinct rows; these pleural chitinized areas usually bearing from two to four tubercles, which are closely approximated basally so as to present a somewhat branched appearance. Male cauda (Plate XVIII, 48) as in Ptychoptera, but dorsal median lobe very short and stout; tubercles on segment immediately before cauda long and slender, similar to those on remainder of abdomen.

Nepionotype.— Ithaca, New York, May 15, 1917.
Neanotype.— Orono, Maine, June 24, 1913.
Paratypes.— With the type pupa.

Malloch's figure of the pupa (1915–17 b: pl. 35, fig. 6) is diagrammatic. It was probably made from a female individual, the antennal sheaths being shorter in this sex than in the male.

FAMILY Rhyphidae

Larva.— Body eucephalous, amphipneustic. Mandibles opposed. Eyespots distinct. Spiracles on sides of prothorax. Thoracic and abdominal segments divided by false constrictions. Spiracular disk surrounded by two or five lobes (Rhyphinae) or by four lobes (Trichocerinae), or unprovided with lobes (Mycetobiinae).

Pupa.—Head with a bilobed setiferous cephalic crest. Palpi stout, straight. Pronotal breathing horns short, not prominent. Tarsal sheaths lying in pairs, one above another, the fore legs lying on the middle legs, and these latter on the hind legs. Lateral abdominal spiracles small but distinct.

The family Rhyphidae includes an apparently heterogeneous group of genera which are in reality very closely related. The adults are of diverse appearance, but the immature stages are exceedingly similar to one another and undoubtedly all three of the groups included in the family are closely allied.

The immature stages of the Rhyphinae (Rhyphus) have been discussed by many entomologists, among others by Johannsen (1910: 35–36,

Rhyphus punctatus) and by Malloch (1915–17b:243, *R. punctatus*). The larvae are often handsomely banded and mottled with brown or purplish. Johannsen and other authors describe the cauda as ending in two short lobes, but Malloch mentions five such lobes. The general structural characters are those described above for the family. The larvae occur in decaying vegetable matter, in manure (especially horse and cow dung), in sewage, and in similar material.

The Mycetobiinae are represented by Mycetobia, a curious fly which superficially resembles a mycetophilid rather than a crane-fly. Long ago Lyonet, Dufour, Guérin-Méneville and others described and figured the larva of Mycetobia and noted the eucephalous condition of the head and the amphipneustic spiracles. Osten Sacken (1863) first suspected the affinities of this genus with Rhyphus. More recently, work by Johannsen (1910:31–32), Malloch (1915–17 a, and 1915–17b:244–245), Edwards (1916), Knab (1916), and others has definitely settled the relationship of this insect with the Rhyphidae. The larvae and the pupae agree closely with the general family characters discussed above. The larvae occur in decaying wood and about fermenting sap in wounds of trees. The genera Ditomyia Winn. and Symmerus Walk. are now placed in a separate family from Mycetobia, the Ditomyiidae (Keilin, 1919).

Until recently, the Trichocerinae have been considered as being members of the family Tipulidae. They include only the genus Trichocera, with about twenty-five nominal species, and, presumably, Ischnothrix Bigot, represented by a single species from Cape Horn. From the general appearance of the adult, these flies have usually been referred to the tribe Limnophilini, in a position near the genus Limnophila. Brunetti (1912) referred them to the Pediciini, and most other recent workers have accorded them tribal or subfamily rank in the Tipulidae. Bezzi (1914:214), influenced by the work of Keilin (1912), referred Trichocera to the Rhyphidae, but later (1918a:20) placed it back in the Tipulidae (as Limnobiidae). Malloch (1915–17b:234) likewise places Trichocera with the Tipulidae, but mentions the close resemblance of the larva to that of Rhyphus. The best discussions of the morphology of the larva and the pupa are those by Keilin (1912) and De Meijere (1916:191–194), both of whom were strongly impressed by the striking resemblance of the larva to that of Rhyphus. In the present paper, the Trichocerinae is the only group considered in detail.

SUBFAMILY **Trichocerinae**

Genus **Trichocera** Meigen (Gr. *hair* + *horn*)

1800 *Petaurista* Meig. Nouv. Class. Mouch., p. 15 (*nomen nudum*).
1803 *Trichocera* Meig. Illiger's Mag., vol. 2, p. 262.
1911 *Paracladura* Brun. Rec. Indian Mus., vol. 6, p. 286.

Larva.— Body eucephalous, amphipneustic. Thoracic segments divided into two annuli. Spiracles on lateral margin of posterior ring of prothorax. Abdominal segments divided into three annuli. Cauda ending in four lobes, ventral lobes the longer and more slender; lobes bearing numerous stout hairs near tips on outer face. Eyespots distinct. Lateral plates of head widely separated on midventral line. Mandible with prostheca distinct.

Pupa.— Cephalic crest small, lobes with stout setae. Clypeus short; labrum dumb-bell-shaped; palpal sheaths stout. Antenna elongate. Leg sheaths lying in pairs above one another, gradually lengthening, fore pair the shortest, posterior pair the longest. Pronotal breathing horns short. Abdominal spiracles small, but distinct and functional.

The small winter gnats of the genus Trichocera are rather familiar, since they are not rare during the winter months in cellars or even in the open on warm days, occurring in sunlit places in small, dancing swarms. They are abundant during fall and spring. They occur also in cool, shady places in summer, but are less in evidence at this season.

Trichocera is found somewhat commonly and regularly in mines, often at very considerable depths. Boheman (1850) records specimens of *T. regelationis* in mines 600 feet below the surface, and Lampa (1890) also records the species as being found at considerable depths. Dr. H. B. Hungerford found numerous adults of a species of Trichocera in the Amethyst silver mine near Creede, Colorado, in 1914. Specimens that he obtained were taken at the sixth level, but the miners said the insects were to be seen in all parts of the mine; along the laterals at the sixth level they were noted 7000 feet from the entrance. It is supposed that these individuals breed in the animal waste which naturally accumulates in such places. Trichocera is also a characteristic inhabitant of caverns and grottoes, all stages being found in such situations (Schmitz, 1909:80; Bezzi, 1911–12:46–47, 49, and 1914:214).

The swarming and mating of these flies is well known. It has been ably described by Ainslie (1907), and is here discussed only in general terms. The insects swarm commonly in the autumn. Sometimes the swarms include but comparatively few individuals, but at other times many thousands participate. They swarm usually from five to twenty-five feet above the ground, all facing in the same direction, that is,

toward the wind or breeze. Mating takes place in the air, and united pairs then fly away or drop to the ground beneath. The swarms are often very dense, and individuals come in frequent contact with one another. When the breeze shifts, the swarm immediately readjusts its position and direction.

The immature stages of Trichocera are spent in decaying vegetable matter, beneath dead or decaying leaves, in débris, in fungi, and in similar situations. Sometimes the larvae and pupae are rather numerous in stored roots and tubers, especially potatoes, in which cases they may assume an economic importance (Johannsen, 1910:34–35; Carpenter, 1912). The specimens used by the writer for study are part of Johannsen's material, determined as *T. regelationis* from Patten, Maine. The taxonomic condition of the group is such that no specific identification of the adult flies can be attempted at this time. The immature stages of the generalized subgenus of Trichocera, Diazosma Bergroth, are unknown.

The most important literature on the genus Trichocera is as follows:

Trichocera regelationis	General	Dufour, 1840:161.
Trichocera regelationis	Larva, general	Schmitz, 1909:80, pl. 8, fig. 3.
Trichocera regelationis	Larva, pupa	Johannsen, 1910:34–35, figs. 51–57.
Trichocera regelationis	Pupa	De Meijere, 1916:194.
Trichocera hiemalis	Larva, general	Curtis, 1846b.
Trichocera hiemalis	General	Cameron, 1917:63.
Trichocera fuscata	General	Carpenter, 1912. (Damage.)
Trichocera sp	Larva	Bremi-Wolf, 1846:175.
Trichocera sp	Larva	Perris, 1847:37, pl. 1, fig. 3.
Trichocera sp	General	Bezzi, 1911–12:46–47, 49.
Trichocera sp	Larva	De Meijere, 1916:191–194, figs. 21–23.
Trichocera sp	Larva, pupa	Keilin, 1912. (Morphology.)
Trichocera sp	Larva	Malloch, 1915–17b:234–235, pl. 26, fig. 1; 306.

Trichocera regelationis, supposition.

Larva.— Length, 8–9.5 mm.
Diameter, 1 mm.

Coloration pale brown in preserved material, whitish in fresh specimens.

Body rather short, cylindrical to slightly depressed (Plate XIX, 49). Pseudopods lacking. Head complete, non-retractile, strongly chitinized; lateral plates of head widely separated on midventral line, connected only by a narrow bridge posteriorly; chaetotaxy as shown (Plate XIX, 52 and 53). Mandibles opposed, of three parts, principal segments bearing on inner side near base an apparently movable appendage (prostheca) which has, besides the large apical tooth, three smaller teeth. Labrum bluntly rounded, with long hairs. Epipharynx with lateral combs of about six blunt teeth. Antenna two-segmented; basal segment

very short, disk-shaped, inserted on a large brown-margined plate which is part of the head chitin; second segment much narrower, egg-shaped; in addition to this segment there are several small sensory papillae on the end of the first segment.

Segments of body divided into secondary annuli, thoracic segments with two such rings, abdominal segments with three; annuli bearing transverse rows of short setae. Anterior spiracles on posterior ring of prothorax near lateral margin conspicuous, smaller than posterior spiracles but constructed on same general principle. Spiracular disk surrounded by four lobes; ventral lobes longer and more slender than dorsal pair, inner face narrowly chitinized, outer face densely clothed with abundant short yellow hairs (Plate XIX, 50 and 51); dorsal lobes shorter and blunter, with short hairs on apices of outer face. Spiracles large, at base of dorsal lobes.

Pupa.— Length, 7.5–7.8 mm.
Width, d.-s., 1.4 mm.
Depth, d.-v., 1.4 mm.

Coloration whitish; head, thorax, and sheaths of appendages brown.

Anterior cephalic crest small, lobes widely separated, each tipped with a long, stout seta directed ventrad; a tiny seta just behind each anterior lobe. Antennal bases above and slightly between the eyes, bent dorsad and thence caudad, passing behind joints of legs, in the female attaining to about one-third length of wing. Frontal region between eyes slightly tumid, somewhat shiny. Clypeus short, the sides parallel, the apex U-shaped; labrum broad, dumb-bell-shaped, the caudal margin concave. Maxillary palpi very short and stout, ending before knee joints of fore legs (Plate XIX, 55). A small tubercle just laterad of base of antenna. Each cheek produced into a long, blunt, wrinkled tubercle.

Mesonotum (Plate XIX, 54) strongly gibbous, pale medially, narrowed in front, anterior margin truncated and sending a sharp median carina cephalad; sides of mesonotum opposite wing root with four small setae, in two slightly separated groups. Anterior angles of pronotum with a short bristle. Breathing horns small, short and almost straight, broad basally, apical half narrow, inner face fused or closely approximated with pronotum, apex cleft. Wing sheaths attaining level of tips of fore tarsi; venation rather distinct. Leg sheaths with fore legs stout; fore tarsi overlying middle tarsi (Plate XIX, 55); middle tarsi overlying hind tarsi; terminal segments of tarsi swollen. Abdominal segments divided into about three false annuli; caudal margin of each segment fringed with short hairs. Tiny abdominal spiracles on pleural segments. Female ovipositor (Plate XIX, 56) with the dorsal valves short, widely separated, acutely pointed; ventral acidotheca elongate, approximated, bent slightly ventrad.

Larvae and pupae.— Patten, Aroostook County, Maine, May 3 and 23, 1907.

FAMILY **Tipulidae**

The family Tipulidae is the largest group of crane-flies, and possibly the only one to which the name is justly applicable. It includes a vast number of species (nearly three thousand), arranged in about one hundred

and forty genera. The species are found in most parts of the world, being restricted only by intense heat and cold. Crane-flies require moisture in order to complete their development, and, as a consequence, are almost always found in the neighborhood of flowing or stagnant water. No species known to the writer are inhabitants of desert conditions, the nearest approach probably being some Eriopterini, such as Helobia, Trimicra, and other genera.

The immature stages frequent very wide ranges of habitat, which are indicated elsewhere (page 716). They are readily separable from other related species by the characters outlined on pages 744 to 758. The subfamilies of Tipulidae may be separated by the following keys:

Larvae

1. Body provided with elongate spines or leaflike projections. **Cylindrotominae,** *pars* (p. 959)
   Body without distinct spines....................2
2. Form depressed, with more or less distinct lateral tubercles; terrestrial on spermatophytic plants.................... **Cylindrotominae,** *pars* (p. 959)
   Form terete; if depressed, without tubercles....................3
3. Spiracular disk surrounded by six or eight lobes.................... **Tipulinae** (p. 974)
   Spiracular disk not as above....................4
4. Spiracular disk surrounded by two, four, or five lobes....................5
   Spiracular disk with three lobes or without distinct lobes....................7
5. Head capsule massive, the hypopharynx a flattened plate with few teeth; size large (aberrant Tipulinae)....................6
   Head capsule massive or dissected, if the former the hypopharynx not as above; size usually small.................... **Limnobiinae,** *pars* (p. 793)
6. Spiracular disk with five lobes; lives in moss....................Genus *Dolichopeza* Curt. (p. 981)
   Spiracular disk with four slender, hornlike lobes; lives in earth. *Tipula selene* Meig. (p. 1016)
7. Size large (30 mm. or over); form very stout, terete; head capsule of the tipuline type; lives in wood....................Genus *Tanyptera* Latr. (p. 988)
   Size small (20 mm. or under); form slender, terete; head capsule of the limnobiine type. **Limnobiinae,** *pars.* (p. 793)

Pupae

1. Basal abdominal segments unarmed with teeth or spinous projections before posterior margin....................2
   Basal abdominal segments armed with a transverse row of usually small teeth or chitinous projections before posterior margin....................3
2. Last larval skin adhering to posterior end, attaching pupa to a plant stem or a leaf; coloration bright green.................... **Cylindrotominae,** *pars* (p. 959)
   Not as above.................... **Limnobiinae,** *pars* (p. 793)
3. Maxillary palpi curved or recurved at tips; size large, usually 12 mm. or over. **Tipulinae,** *pars* (p. 974)
   Maxillary palpi not recurved at tips....................4
4. Maxillary palpi long, slightly or decidedly curved at tips; size large, length usually 12 mm. or over....................5
   Maxillary palpi short, straight; size small, usually 10 mm. or under. **Limnobiinae,** *pars* (p. 793)

5. Dorsal abdominal segments with two slender spines before margin. **Cylindrotominae,** *pars* (p. 959)
   Dorsal abdominal segments with four or more teeth or spines before margin. **Tipulinae,** *pars* (p. 974)

SUBFAMILY **Limnobiinae**

The subfamily Limnobiinae includes a vast assemblage of usually small crane-flies. Only a few genera approach the ordinary size of the other principal subfamily, the Tipulinae, such genera being Limnobia, Psaronius, Limnophila, Eriocera, Pedicia, and a few others.

The writer has endeavored to key the immature stages of tribes, subtribes, and genera. As has been stated elsewhere, the keys are based almost entirely on material seen by the writer, and additional specimens of other species will undoubtedly modify the arrangement very considerably. It is believed, however, that the keys as given will at least furnish suggestions or a basis for succeeding work. The characters given in the keys, in so far as is possible, are those that can be seen without making a detailed dissection of the specimen. However, for most species it is necessary to study the larval head, as already outlined (page 741). The character of " head massive " or " head rodlike " can often be detected thru the larval integument without dissection. The spiracular disk is usually studied without especial difficulty.

The immature stages of the majority of the species are spent in moist earth, usually near water. Some are nearly, if not quite, aquatic (Antocha, Elliptera, some Dicranomyia); others are fungicolous (Ula, some Limnobia); several live under the bark of trees (some Dicranomyia, some Rhipidia, Discobola, Gnophomyia, Teucholabis, Elephantomyia, and others); one, at least, mines in the leaves of plants (Dicranomyia).

The habits of the various genera and species are discussed in greater detail under the respective titles. The following keys separate the tribes and the subtribes of the subfamily Limnobiinae:

Larvae

1. Spiracular disk provided with two long ventral lobes 2
   Spiracular disk not as above 3
2. Spiracles lacking or vestigial; mentum not completely divided medially; hypopharynx a chitinized double comb; species aquatic, in silken cases. *Limnobiini*, subtribe *Antocharia* (p. 799)
   Spiracles large, prominent, exposed; mentum completely divided medially; hypopharynx labriform . . . . *Pediciini* (p. 894)
3. Spiracular disk surrounded by four or five lobes 4
   Spiracular disk surrounded by three lobes or without distinct lobes 19

4. Head capsule massive, compact, the posterior incisions usually shallow..........5
Head capsule of four or six slender rods, the posterior incisions profound..........15
5. Mentum completely divided, a toothed plate on either side; abdominal segments without distinct creeping-welts..........6
Mentum, if present and chitinized, not completely divided; abdominal segments with basal creeping-welts..........8
6. Spiracular disk squarely truncated, surrounded by five lobes........*Eriopterini* (p. 908)
Spiracular disk with four lobes..........7
7. Each mental plate four-toothed; hypopharynx labriform.
Pediciini, subtribe *Adelphomyaria* (p. 895)
Each mental plate with seven or eight teeth; hypopharynx a comblike ring.
Hexatomini, subtribe *Pseudolimnophilaria* (p. 848)
8. Spiracular disk with five lobes..........9
Spiracular disk with four lobes..........12
9. Antennae almost globular, with two conical apical papillae; lives in fungi.
Hexatomini, subtribe *Ularia* (p. 838)
Antennae elongate-cylindrical..........10
10. Abdomen with dorsal and ventral creeping-welts; mentum with more than five teeth.
Limnobiini (p. 795)
Abdomen with six ventral welts only; mentum with five or fewer teeth..........11
11. Mentum five-toothed; lives in earth........*Limnobiini*, subtribe *Rhamphidaria* (p. 830)
Mentum three-toothed; lives in wood.....*Hexatomini*, subtribe *Epiphragmaria* (p. 843)
12. Antennae almost globular, with two conical apical papillae; lives in fungi.
Hexatomini, subtribe *Ularia* (p. 838)
Antennae elongate-cylindrical..........13
13. Abdomen with dorsal and ventral creeping-welts, the latter naked; mentum not three-toothed; forms aquatic..........*Limnobiini*, subtribe *Ellipteraria* (p. 806)
Abdomen with ventral creeping-welts only; mentum with only three primary teeth; species not aquatic..........14
14. Form long, slender; skin naked, shiny, transparent; apical segment of antennae elongate, as long as, or longer than, basal segment; mentum with a smaller tooth on either side; lives in earth..........*Limnobiini*, subtribe *Dicranoptycharia* (p. 828)
Form short, stout; skin white, opaque; apical segment of antennae short, hemispherical; mentum without small lateral teeth; lives under bark.
Hexatomini, subtribe *Epiphragmaria* (p. 843)
15. Blades of maxillae not produced; form long and slender..........16
Blades of maxillae produced into flattened elongate appendages, the tips of which protrude from the thoracic orifice when the head is completely retracted; form short and stout..........17
16. Spiracular disk squarely truncated, surrounded by five lobes which are fringed with numerous, usually short, hairs; esophageal region not conspicuously grooved.
Eriopterini, subtribe *Eriopteraria* (p. 911)
Spiracular disk surrounded by four lobes, each ventral lobe with a single elongate bristle; esophageal region elongate, grooved; lives under bark.
Eriopterini, subtribe *Elephantomyaria* (p. 952)
17. Mental region a narrow, transverse, chitinized bar.
Hexatomini, group *Limnophilae* (p. 858)
Mental region not chitinized..........18
18. Mandibles hinged; maxillae and labrum densely hairy; dorsal plates of head capsule united into a spatula..........*Hexatomini*, group *Ulomorphae* (p. 869)
Mandibles not hinged; maxillae and labrum not densely hairy; dorsal plates of head capsule separated..........*Hexatomini*, subtribe *Hexatomaria* (p. 876)
19. Head capsule massive, compact..........20
Head capsule of six slender rods; lives under bark.
Eriopterini, subtribe *Eriopteraria* (p 911)

20. Mental plates not completely divided; abdominal segments with basal creeping-welts on both ventral and dorsal surface; spiracular disk indistinctly four- or five-lobed. *Limnobiini* (p. 795)
Mental plates completely divided; abdominal segments without welts; spiracular disk obliquely truncated.. *Eriopterini* (p. 908)

Pupae

1. Pronotal breathing horns eight-branched; forms entirely aquatic. *Limnobiini*, subtribe *Antocharia* (p. 799)
Pronotal breathing horns simple, unbranched.......................................2
2. Rostral sheath elongated; lives in wood. . *Eriopterini*, subtribe *Elephantomyaria* (p. 952)
Rostral sheath not elongated.......................................3
3. Pronotal breathing horns very minute, conical, visible only with a lens.[5] *Limnobiini*, subtribe *Dicranoptycharia* (p. 828)
Pronotal breathing horns larger, not microscopic.......................................4
4. Dorsal spiracles on eighth abdominal segment large and functional.......................................5
Dorsal spiracles on eighth abdominal segment small or lacking.......................................7
5. A large circular spinous area on abdominal pleurites; cephalic crest chitinized, acutely pointed; pronotal breathing horns directed ventrad; lives in decaying wood. *Hexatomini*, subtribe *Epiphragmaria* (p. 843)
Not as above.......................................6
6. Pronotal breathing horns large, flattened, the tips yellow; abdominal tergites with shagreened crossbands....................... *Hexatomini*, subtribe *Ularia* (p. 838)
Pronotal breathing horns slender, cylindrical; abdominal tergites with tranverse rows of small spines.......................... *Limnobiini*, subtribe *Rhamphidaria* (p. 830)
7. Abdominal pleurites with circular areas set with numerous microscopic spicules; pronotal breathing horns short, usually truncated at tips, which are margined with the breathing pores....................................... *Pediciini* (p. 894)
Abdominal pleurites not as above, if with spines these large and few in number; pronotal breathing horns long, cylindrical.......................................8
8. Abdominal segments with broad transverse bands or welts on basal rings of third to seventh tergites....................................... *Limnobiini* (p. 795)
Abdominal segments with basal ring unarmed as above, posterior ring before margin with a transverse row of spines or stiff setae.......................................9
9. A distinct crest on mesonotal prescutum armed with tubercles, spines, or setae; size small (usually under 9 mm.)................................. *Eriopterini* (p. 908)
No distinct crest on mesonotal prescutum (scutellum armed in some Eriocera); size large (usually over 10 mm.).......................................10
10. Leg sheaths very short, barely exceeding wings; lives under bark. *Eriopterini*, genus *Gnophomyia* (p. 934)
Leg sheaths longer, extending one or more segments beyond tips of wings...........11
11. Size small (under 6 mm.); abdominal armature weak, lacking on segment 7. *Pediciini*, subtribe *Adelphomyaria* (p. 895)
Size larger; abdominal armature stronger, spinous; if small in size (Dicranophragma), basal annuli of abdominal segments armed with naked tubercles. . *Hexatomini* (p. 835)

Tribe **Limnobiini**

A large group of crane-flies, arranged in a few often extensive genera, comprise the tribe Limnobiini. At first sight the tribe appears to be a

[5] In the genus Cladura (Eriopterini), reared while this paper was going thru the press, the breathing pores are likewise microscopic, being entirely sessile (page 949).

heterogeneous assemblage, but in reality it constitutes a natural group. The tribe as herein arranged includes the old group Limnobiini, with the addition of several genera that were formerly distributed in the Antochini. The divisions of the tribe as now constituted are as follows:

1. Limnobaria — including the old tribe Limnobiini.
2. Ellipteraria — including the genus Elliptera. This is close to the preceding subtribe and may be a group belonging to it.
3. Antocharia — including Antocha and presumably allied genera, as Orimargula, Orimarga, Diotrepha, and possibly others.
4. Rhamphidaria — including Rhamphidia and its allies.
5. Dicranoptycharia — including Dicranoptycha only.

These groups are not far removed, phylogenetically, from the lowermost divisions of the Hexatomini, such as the Ularia and the Epiphragmaria, and the two tribes are unquestionably closer together than their arrangement on paper would indicate. The separation of the two major groups was made largely on the characters of the imagines.

The larvae have the body terete, moderately elongate or very long and slender (Dicranoptycha). The abdominal segments are subdivided into a basal and a posterior ring, the former with transverse welts of microscopic chitinized points or hooks. In the Limnobaria and the Antocharia these welts occur on both the dorsal and ventral surfaces in the form of microscopic hooks; in the Ellipteraria they are on segments 3 to 9 on the dorsal surface only, being indicated on the ventral surface but naked; in the Rhamphidaria the welts are ventral in position on segments 2 to 7; in the Dicranoptycharia they are similar, on segments 2 to 8. The body in Dicranoptycha is entirely glabrous.

The head capsule is of moderate to large size and is massive and compact, consisting of a narrow dorsal plate which is usually indented behind, and two broad mussel-shaped lateral plates which are connected anteriorly across the venter to form the mental plate. The mental plate consists of an outer plate which usually terminates in a single median point, and behind this an inner plate which contributes additional teeth to the mentum. In Dicranoptycha there is but one subequal tooth on either side, with an additional much-reduced tooth; in Rhamphidia there are two teeth, and in the other groups there are usually four or five. The hypopharynx is usually a double plate united at the ends to form a collar, with the anterior margins finely toothed. The maxillae are

large and simple in structure; the cardo and stipes are large; the palpus is flattened. The antennae have the apical segment or papilla ranging from elongate, in Dicranoptycha, to very flattened and disklike, in Limnobia and its allies. The mandibles are usually of simple structure, with one or two dorsal teeth and from three to seven teeth in the ventral cutting row.

The spiracles are lacking in some species, at least, of Antocha. The spiracular disk is surrounded in Rhamphidia by five subequal lobes, in Dicranoptycha by four slender, naked lobes; in many Limnobaria the lobes are lacking or indistinct.

The larvae of many of the species are able to spin silken cocoons or tubes in which they live. These tubes are open at both ends, and are usually covered exteriorly with particles of extraneous matter gathered in the larval haunts.

The pupae usually lack a distinct setiferous cephalic crest, altho one is present in Rhamphidia and in Dicranoptycha. The pronotal breathing horns are usually large, and are either subcircular, or wider than long (most Limnobaria), rarely elongate (Rhamphidaria), very large, earlike, and contiguous or practically so on the median line (Ellipteraria), or branched into eight long filaments (Antocharia); in the Dicranoptycharia, however, they are microscopic. The abdominal segments on the basal ring often show a transverse welt of small hairs or a double convergent row of chitinized hooks; in Discobola, Rhamphidia, and Dicranoptycha, however, this is apparently not the case, the abdominal armature being more eriopterine or hexatomine in appearance. The eighth abdominal segment often bears a pair of dorsal spiracles; these are apparently lacking in some species (*Antocha saxicola*) and are small in most Limnobaria, but are large and functional in Rhamphidia.

The following keys separate the subtribes of the tribe Limnobiini:

Larvae

1. Body ending in two long ventral lobes; spiracles lacking or very reduced; forms strictly aquatic . . . . *Antocharia* (p. 799)
   Body not as above; spiracles large 2
2. Body with ventral and dorsal welts on abdominal segments 3
   Body with ventral welts only 4
3. Spiracular disk surrounded by four lobes which are provided with long fringes of hair; dorsal welts microscopically spiculose; ventral welts naked; species aquatic. *Ellipteraria* (p. 806)
   Spiracular disk not as above; dorsal and ventral welts alike . . . . *Limnobaria* (p. 808)

4. Body moderately elongated, covered with a long, dark pubescence; abdomen squarely truncated at end, surrounded by five lobes, presenting an eriopterine appearance; mentum conspicuously five-toothed .... *Rhamphidaria* (p. 830)
   Body very long and slender, glabrous; abdomen surrounded by four narrow, glabrous lobes; mentum indistinctly five-toothed .... *Dicranoptycharia* (p. 828)

Pupae

1. Pronotal breathing horns branched; forms entirely aquatic .... *Antocharia* (p. 799)
   Pronotal breathing horns simple 2
2. Pronotal breathing horns very tiny, microscopic, conical .... *Dicranoptycharia* (p. 828)
   Pronotal breathing horns large, conspicuous 3
3. Pronotal breathing horns large, earlike, contiguous basally; forms aquatic, in silken cocoons .... *Ellipteraria* (p. 806)
   Pronotal breathing horns not contiguous basally 4
4. Cephalic crest small or lacking; pronotal breathing horns short and broad, rarely elongated; a pair of small spiracles on dorsum of eighth abdominal segment.. *Limnobaria* (p. 808)
   Cephalic crest large, setiferous; pronotal breathing horns long and slender, cylindrical; a pair of large spiracles on dorsum of eighth abdominal segment. *Rhamphidaria* (p. 830)

The most important literature on the tribe Limnobiini is as follows:

Antocha saxicola	General	Needham, 1908a:205.
Antocha sp	Larva	Malloch, 1915–17b:236–237.
Elliptera omissa	Larva, pupa, general	Mik, 1886b.
Elliptera omissa	Larva, pupa	Grünberg, 1910:31–32. (Copy.)
Elliptera omissa	Larva, pupa	Malloch, 1915–17b:226–227.
Thaumastoptera calceata	Larva, pupa, general	Lenz, 1920a.
Limnobia quadrimaculata	General	Von Röser, 1834 (as *annulus*).
Limnobia quadrimaculata	Larva, pupa	Beling, 1873b:590–591 (as *annulus*).
Limnobia bifasciata	Larva, pupa, general	Bremi-Wolf, 1846 (as *xanthoptera*).
Limnobia bifasciata	Larva, pupa, general	Pastejrík, 1909 (as *xanthoptera*).
Limnobia bifasciata	Larva, pupa	De Meijere, 1916:198–201.
Limnobia decemmaculata	General	Loew, 1873:41.
Limnobia decemmaculata	General	Verrall, 1912.
Limnobia flavipes	Larva	Beling, 1886:202.
Limnobia inusta	General	Beling, 1886:202 (as *macrostigma*).
Limnobia sexpunctata	Larva	Beling, 1879:54–55 (as *nigropunctata*).
Limnobia nubeculosa	General	Beling, 1879:56.
Limnobia obscuricornis	Larva, pupa	Beling, 1879:55–56.
Limnobia tripunctata	Larva, pupa	Beling, 1873b:591–592.
Limnobia triocellata	Larva, pupa, general	Johnson, 1906:2.
Limnobia triocellata	Larva, pupa	Malloch, 1915–17b:215–216.
Limnobia immatura	Pupa	Malloch, 1915–17b:216.
Libnotes perkinsi	General	Perkins, 1913:clxxxii (as Limnobia).
Discobola caesarea	Pupa	Mik, 1884.
Dicranomyia trinotata	Larva, pupa	Thienemann, 1909.
Dicranomyia trinotata	Larva, pupa	Grünberg, 1910:29. (Copy.)
Dicranomyia dumetorum	General	Winnertz, 1853.

Dicranomyia dumetorum	General	Beling, 1873 b: 592.
Dicranomyia dumetorum	General	Beling, 1879: 56.
Dicranomyia dumetorum	Larva	Beling, 1886: 201–202.
Dicranomyia sp.	General	Schubart, 1854.
Dicranomyia foliocuniculator	General	Swezey, 1913.
Dicranomyia foliocuniculator	Larva, pupa	Swezey, 1915: 87.
Dicranomyia umbrata	Larva	De Meijere, 1916: 197–198.
Dicranomyia simulans	Larva, pupa, general	Needham, 1908 a: 214–217.
Dicranomyia simulans	Larva, pupa	Malloch, 1915–17 b: 213–214.
Rhipidia maculata	Pupa	Beling, 1873 b: 592.
Rhipidia maculata	Larva, general	Beling, 1879: 52–53.
Rhipidia uniseriata	Larva, general	Beling, 1879: 53–54.
Rhipidia domestica	General	Johnson, 1910: 704.
Dicranoptycha winnemana	Larva, pupa	Alexander, 1919 b.
Rhamphidia longirostris	General	Gercke, 1884.
Rhamphidia longirostris	General	Grünberg, 1910: 30. (Copy.)
Rhamphidia flavipes	Larva	Hart, 1898 [1895]: 197–199.
Rhamphidia flavipes	Larva	Malloch, 1915–17 b: 231–232.

Subtribe **Antocharia**

The subtribe Antocharia includes the genus Antocha and probably three or four related genera, such as Diotrepha, Orimarga, and Orimargula. The group is well-defined in all stages, so far as these are known, the larvae presenting a curious superficial resemblance to those of Pedicaria, while the pupae introduce a novelty of structure of the breathing horns, which is discussed in detail elsewhere (page 805). It is probable, however, that these peculiarities of larval and pupal structure are largely the result of habit and habitat, and a critical survey of the structure shows a close relationship with the other subtribes herein recognized.

Genus **Antocha** Osten Sacken (Gr. *close approximation*)

1859 *Antocha* O. S. Proc. Acad. Nat. Sci. Phila., p. 219.

Larva.— Body slender, tapering behind, ending caudally in two elongate ventral lobes which bear a few hairs at their tips and at intervals along their length. Abdominal segments 2 to 7 each with a swollen area on basal ring densely covered with microscopic hairs. Tracheal gills four in number, large, constricted into three or four lobes. Spiracles lacking or rudimentary. Head capsule moderate in size. Mentum with nine or ten teeth, deeply split behind. Maxilla conspicuous, consisting of two subequal lobes which are provided with dense brushes of hairs. Hypopharynx with chitinized teeth.

Pupa.— Anterior end of body large, tapering behind. Head with a small median lobe in front, on either side of which is a small tubercle; genae gibbous. Pronotal breathing horns large, flattened, the margin branching into eight long filaments. Abdominal segments on basal ring with a double transverse row of small hooks which converge at the ends to inclose an oval depressed area; last segment of body terminating in two strong, recurved, chitinized hooks.

Antocha is a small genus of crane-flies (about seven species) whose specific limits are still not well understood. The species are well distributed thruout the Northern Hemisphere. The adult flies are of primitive organization, but the larvae and the pupae are highly specialized in many respects.

The only previous record of the immature stages of any member of this group is the unknown Limnobiine No. 2 (Malloch, 1915–17b: 236–237), which surely refers to an Antocha, possibly *A. monticola* Alex. The main point of difference between the species described by Malloch and the species described in detail hereinafter is the small spiracles mentioned in the description of the former species. *A. saxicola* lacks spiracles, since it has no use for them, being confined to submerged cases often many feet below the surface of the water.

Altho nothing is known concerning the immature stages of the genera Orimargula, Orimarga, and Diotrepha, the writer believes that these genera will be found to have larvae of this same general type, since from the structure of the adults they are obviously derived from the Antocha stem. The larvae are curiously suggestive of the Pediciini (as compared with Dicranota), but the structure of the mouth parts, the smooth pseudopods, and the cauda, are quite different and indicate that the similarities are analogous only. The pupae are unlike those of any crane-fly as yet made known, in the very remarkable breathing horns; but this is possibly a condition brought about by the habitat rather than a fundamental feature. The apparently very different pupae of Elliptera are closely related to Antocha.

Antocha saxicola O. S.

1859 *Antocha saxicola* O. S. Proc. Acad. Nat. Sci. Phila., p. 219.

Antocha saxicola has one of the most interesting life histories of any of the crane-flies yet discovered, not only because of the larval and pupal habitat, but also because of the peculiar structures that appear in the larva and in the pupa and have been found nowhere else in the immature stages of the family, so far as is known. The larvae simulate strikingly the same stage in the Pedicaria, but are apneustic, entirely lacking functional spiracles and depending wholly on tracheal gills for their respiration. The pupae have the pronotal breathing horns split into eight long filaments, so that they bear a curious superficial resemblance to the pupae

of the black fly (Simuliidae). Both larvae and pupae spend their entire lives in cases on stones in water — usually in running, well-aërated water, and often in the most rushing torrents.

The larvae, as already stated, lack spiracles, the entire respiration being carried on thru tracheal gills, four in number, and the rich tracheal development in the elongate caudal lobes. Thus the trâcheal system is truly closed, and represents the maximum of specialization in the reduction in size and final loss of the spiracles. In air-breathing, terrestrial forms, the spiracles are large and situated comparatively close together, gradually becoming smaller and more removed from one another as the creature becomes more and more dependent on blood gills or tracheal gills for respiration. This is the only truly closed tracheal system known to the writer to occur in the Tipulidae. It should be noted that the loss of the spiracles is accompanied by great enlargement of the gills and the taking on of the gill function by the two caudal lobes. The haunt of the larvae is in silken cases on rocks, often in the swiftest part of the stream, where it is impossible to breathe thru spiracles and where the associated forms of life (Ephemerida, Plecoptera, Trichoptera, and Diptera) all, or practically all, depend entirely on gills for respiration.

As a rule, the larval cases are made on rubble or rounded stones, a crevice or a groove caused by inequalities of the rock surface covered over being the simplest and commonest place chosen. The inequalities in the rock are bridged over by a silken, mud- or silt-covered case, which is very delicate and laterally fimbriated with the young larva but becomes much firmer, thicker, and more compact with the older larva and pupa. The larval case is open at both ends and the larva passes backward and forward freely, showing considerable agility when disturbed. When the larva is still small, the case is correspondingly small and insignificant; but the case of the matured larva is conspicuous, measuring from 4 to 5 centimeters in length and about 1.2 centimeters across the lateral "wings," or fimbriations. The insect moves freely along the tube but is very loath to leave it unless actually ejected. As stated above, the late larval and pupal covering is very different from the flimsy, silt-covered tube of the young larva, being smooth, compact, hard, and often covered with pebbles. The pupa has two powerful hooks at its caudal end, enabling it to fasten to the case. In most cases the pupa hangs with the current, head downstream, like the pupa of Blepharocera

and unlike the somewhat similar-appearing pupa of the Simuliidae, which rests with the head upstream, against the current, the pupal case being open at the cephalic end only.

These curious larvae were first noted at Ithaca, New York, in mid-April, in Cascadilla Creek. They were common in situations such as described above. Larvae were found thruout most of April, May, and June; they would probably be seen in somewhat fewer numbers thru most of the summer season, since the adult flies have a long seasonal appearance. The first pupa was found on May 15, 1917, but the season that year was very backward and undoubtedly the species pupates earlier in more nearly normal seasons.

In Cascadilla and Fall Creeks, at Ithaca, the immature stages of Antocha are usually associated with a fauna of rapid-water (lotic) forms, the following being the more notable and constant:

Planarians.	*Planaria* sp.
Ephemeridae.	Nymphs of Baetis, Leptophlebia, Ephemerella, Ecdyurus, Epeorus, Iron, Heptagenia, Chirotenetes, and others.
Perlidae.	Nymphs of Pteronarcys, *Perla immarginata* Say, Acroneuria, Neoperla, and others.
Trichoptera.	Larvae and pupae of Helicopsyche (abundant), Hydropsyche, Hydropsychodes, Ithytrichia, Rhyacophila, Leptocerus, Polycentropus, and others.
Lepidoptera.	Larvae and pupae of Elophila.
Coleoptera.	Larvae of Psephenus.
Diptera.	Larvae and pupae of Blepharocera, Simulium, Orthocladius, Tanytarsus, and others.

Early in spring the rocks are plastered with dense coatings of Diatomaceae (Navicula, Synedra, Meridion, and other genera), which later in the season become much rarer or disappear entirely. It is often impossible to tell the case of Antocha from that of some very similar caddis-worm cases, especially some of the glossosomatine Rhyacophilidae. Dr. Noyes found larvae of Antocha in a small, rapid-flowing stream near Ringwood Hollow, and here the cases were covered with tiny pebbles and it was quite impossible to distinguish them superficially from associated caddis-worm cases. In Cascadilla Creek the little cases of Helicopsyche often plaster the upper surfaces of submerged rocks, and the writer has found tubes of Antocha that were almost buried beneath these cases.

Antocha is by no means confined to rapidly flowing streams, altho the insects are very often found in such situations. The writer has found adults in his tent traps set over the Sacandaga River, in Fulton County, New York, where the water was very quiet and at least ten feet deep. Needham (1908a:169–170, 205), similarly, found adults in numbers in his tent traps set over Beaver Meadow Brook at Old Forge, New York, in August, 1905, but did not locate the larvae. In rapid-flowing streams the insects sometimes occur just at the surface in a few millimeters of water, or at greater depths. The immature stages seem adapted to live under almost any conditions of current, from moderate pressure to situations where the water rushes by in torrents and where but few of the usual lotic organisms, such as Blepharocera, Simulium, Psephenus, and others, can exist. From Clemens' studies (1917:14–23) it is evident that the current is much more rapid just beneath the surface than at various lower depths, so that at a depth of one foot the current velocity is only about two-thirds of that at the surface. Thus these aquatic organisms are not constantly and entirely subjected to such tremendous pressures as on first sight they appear to be. Many of the larvae and pupae perish from desiccation, due to the lowering of the stream level and the consequent exposure of the rocks on which their homes are made.

Copulation between the adult flies takes place on the exposed rocks in and along the margins of the streams where the larvae live (Osten Sacken, 1869:127). The eggs are deposited in the water, and the entire life, until the emergence of the adult fly, is spent beneath the water. The whole life cycle may require a year, altho the species is possibly double-brooded. At a single time, and even on a single rock, larvae of various sizes, from very small ones to those almost fully grown, may be found, and this probably explains the long flight-period of the adult. That the species is double-brooded remains to be proved.

The food of the larva consists of microscopic plant organisms in the water, the curious maxillae, with their dense brushes of long hairs, undoubtedly being an adaptation for this type of food.

Larva.— Total length, 9.5–10.5 mm.
Length of caudal lobes alone, 1.1–1.2 mm.
Diameter of body, 1–1.1 mm.

Coloration of living larva, light greenish brown above, clearer greenish ventrally; contents of alimentary canal showing clearly thru the thin skin; on segments 7 and 8, two paired, bright

orange bodies which are very conspicuous, these possibly being fatty in nature; welts on the abdomen dark brown; in preserved specimens general coloration fading to a dull yellow.

Form elongate (Plate XX, 57), tapering behind. Surface with a dense, appressed pubescence and scattered erect hairs. Prothorax long, narrowed in front, anterior orifice margined with dense, fine pubescence; sides of prothorax with numerous long, erect, pale hairs. Mesothorax and metathorax indistinctly divided into two approximately equal annuli; anterior annulus with a few lateral setae. First abdominal segment short, the setae arranged as follows: dorsal, two small grouped setae near posterior margin, laterad of each of these, but in alinement, a solitary stout seta, proximad of each of these a stout seta, and cephalad of each of these another strong seta, the principal setae of each side thus forming a rough triangle; a long, delicate pleural seta on each side; ventral, two small groups of setae, with an arrangement similar to that of the grouped setae of dorsum. Abdominal segments 2 to 7 each indistinctly divided into two annuli by a transverse constriction, the anterior ring about half the length of the posterior ring and bearing medially a transverse elongate-oval (dorsal) to short-oval (ventral) welt, covered with microscopic points; ventral welts very convex and swollen; pleura with a long seta; posterior ring with setae arranged as described above for first abdominal segment; setae of posterior segments of body longer, but occupying same relative position; small solitary inner seta of dorsal posterior line becoming large and prominent on seventh segment; segment 8 with six powerful setae in alinement on ventral surface, situated at base of gills, two being pleural and four ventral in position; dorsum of segment 8 with a rounded median lobe. Gills four, long, delicate, divided into lobes by constrictions (the two caudal lobes, as well as the gills, have taken on a respiratory function). Caudal ventral lobes two (Plate XXI, 68) very long, parallel, with scattered setae arranged as follows: at tips, six or seven; at about two-thirds length, three; at about one-third length, a tuft of from fifteen to twenty long and short setae on lateral and dorsal faces; a small solitary seta, dorsal in position, at base of lobe; a similar bristle on ventral face at about midlength of lobe. Like remainder of body, cauda covered with an abundance of delicate appressed pubescence; on dorsal side, at base of each lobe, a rounded spot, and just inside this a narrow, longitudinal line which is destitute of pubescence. Only dorsal lobe the median one of eighth segment, mentioned above. Spiracles lacking.

Head capsule (Plate XX, 58) moderate in size. Lateral plates thin, double, inner one the longest, outer one forming mental plate. Dorsal plate broad in front, narrowed behind, posterior margin bluntly notched; in front of this plate, two broad plates, rather widely separated medially, presumably belonging to clypeus. Labrum broad, cephalic margin and ventral face with transverse rows of short hairs. Mentum (Plate XX, 59) conspicuous, deeply split behind but not entirely divided as in the Pediciini; an outer flattened, circular median lobe whose outer face is covered with small, scalelike roughenings; behind (dorsad of) this outer lobe the mentum proper, roughly triangular in outline, conspicuous, margin with a broad, blunt, median tooth which is sometimes (Plate XXI, 66) bilobed to form two subequal apical teeth; besides this median tooth, four lateral teeth, the outermost one broad with its lateral angle rounded. Hypopharynx (Plate XXI, 64) forming a ring into which ducts of salivary glands open; anterior part, somewhat resembling mentum in shape, a narrow blade with anterior margin having about eight teeth; posterior part a transverse, arcuated band with anterior margin having about twenty teeth. (In the figure, the two parts of the hypo-

pharynx are shown diagrammatically and separated; in some specimens the lateral teeth are more acute, in others they are more rounded.) Antenna (Plate XXI, 65) elongate, cylindrical, chitinized, apex pale, with two long, sensory setae and a few papillae. Mandible (Plate XXI, 63 and 67) strong, flattened, with two powerful bristles on back, or scrobal region, near base; inner face concave, tip ending in a long tooth, dorsad of apex a single smaller tooth, ventral cutting edge with four gradually smaller teeth, beyond the last of which the margin is crenulated into four or five indistinct carunculations; viewed from inside, lateral teeth appearing blunt. Maxilla (Plate XXI, 63) large, consisting of two elongate-oval lobes, the inner one densely hairy; palpus, borne at tip of outer lobe on ventral face, shaped like one-half of a cylinder split lengthwise, several tiny hyaline sense pegs at apex; laterad of palpus and nearer base of outer lobe, a small elongate sensory tubercle with hairs at apex; inner lobe of maxilla subequal in size and length to outer lobe, but more densely hairy; on its ventral face, four or five long sensory tubercles which are expanded at their ends into setiferous heads; at base of maxilla, a long, slender arm with three setiferous punctures at apex and another puncture at about two-thirds length; setae of this arm very long and delicate. (A dorsal view of the larva is shown in Plate XX, 57.)

Pupa.— Length to tip of cephalic crest, 6.2–6.8 mm.
Width, d.-s., 1.4–1.5 mm.
Depth, d.-v., 1.1–1.2 mm.

Head, thorax, and sheaths of appendages dark brown in fully colored individuals; abdomen pale yellowish white; terminal hooks of abdomen heavily chitinized.

Head on margin above eyes with a blunt median lobe and on either side a small but prominent tubercle; gena gibbous. Compound eyes large, semicircular in outline. Front between eyes with margins almost parallel. Labrum with apex truncated or indistinctly bilobed. Labial lobes broad, appearing subtriangular. Sheaths of maxillary palpi not greatly elongated, slender, cylindrical.

Pronotal breathing horns (Plate XX, 61) flattened at base, each arcuated basally behind, bending laterad to form a concave hollow in front; base dark brown, chitinized, branched into eight long, pale filaments which are grouped more or less in pairs; the two ventral and the four dorsal filaments arising from a short common base, the other two being separate for their entire length; these filaments as long as, or longer than, antennal sheaths, varying in length from rather short to a longer type. Thoracic dorsum broad, ample, feebly wrinkled transversely. Leg sheaths (Plate XX, 60) with all the tarsi very long and slender, reaching almost to end of fifth abdominal segment. Wing sheaths comparatively narrow, reaching base of third abdominal segment; anal angle sharp; venation fairly distinct.

Abdomen pale. Intermediate abdominal segments divided into two annuli, the posterior ring much the larger; dorsa of segments 3 to 6 (Plate XXII, 71), and sternum of segment 6, each with basal annulus tumid and with two transverse rows of small hooks converging at the ends to inclose a linear depressed area; these areas capable of contraction, so that the hooks of each row are united or approximated with those of the opposite row; from thirty to thirty-five hooks in each row, anterior row with hooks directed backward, posterior row with hooks directed forward; on seventh segment, only the anterior row of hooks present, very slightly arcuated, the lateral hooks smaller than those near middle of row; caudad of this

row on segment 7, a darkened, transversely rectangular area bearing setiferous punctures in two broken rows, the posterior row the more complete; posterior rings of other segments of dorsum bearing setae in somewhat the same arrangement. Pleural area pale, segments 2 to 8 with a long, delicate seta on each annulus. Dorsum of segment 8 (Plate XXII, 70) with a large setiferous tubercle on either side, this tubercle densely covered with hairs that are longest behind and shorter in front; caudad of these large, blunt knobs, a slender, setiferous tubercle. Last segment with tergal valves chitinized, elongate, extreme posterior margin rounded medially and feebly bilobed, lateral angles produced caudad and dorsad into powerful curved, heavily chitinized hooks; a few setae at about midlength of these hooks (Plate XX, 62). Sternal valves shorter, slightly bilobed medially.

Nepionotype.— Ithaca, New York, June 4, 1917.
Neanotype.— With the nepionotype.
Paratypes.— Topotypic, May 1 to June 10, 1917.

Subtribe **Ellipteraria**

The present knowledge of the immature stages of the genus Elliptera is due entirely to the work of Mik (1886 b). From his rather detailed description and figures, it certainly appears that the group should receive coordinate rank with Antocharia, Limnobaria, and other divisions herein created. The genus Elliptera shows peculiarities of structure in all stages, but many features of its organization remind one forcibly of species of Dicranomyia (such as *D. simulans* and *D. trinotata*) on the one hand, and of Antocha on the other; and it may be that the genus Elliptera stands in closer relationship to Dicranomyia than is now believed.

Genus **Elliptera** Schiner (Gr. *I omit,* or *ellipse* + *wing*)

1863 *Elliptera* Schin. Wien. Ent. Monatschr., vol. 7, p. 222.
1913 *Ellipoptera* Bergr. Ann. Mag. Nat. Hist., 8th ser., vol. 11, p. 576 (correct spelling).

Elliptera is a small genus, including but five species which have a discontinuous range, two being found in Europe and three in western North America. The commonest of the North American species, *E. clausa* O. S., was found on wet moss in the spray of Vernal Falls, Yosemite Valley, California (Osten Sacken, 1877 : 198). The only information available on the immature stages of a member of this genus is that furnished by Mik (1886 b) on the European species *E. omissa* Egg. (quoted subsequently by Grünberg, 1910 : 31–32, and by Malloch, 1915–17 b : 226–227). The description and account as given below are based entirely on Mik's paper.

Elliptera omissa Egg.

1863 *Elliptera omissa* Egg. Verh. Zool.-Bot. Ges. Wien, vol. 13, p. 1108.

Specimens of *Elliptera omissa* were found by Mik (1886 b) along water-courses and near falls in mountainous regions. The adult flies were noted as late as September 10, swarming about the waterfalls.

Larvae and pupae were found on July 30 and August 17 near Salzburg, upper Austria, living in elongate and somewhat depressed cocoons about 10 millimeters long and 4 millimeters broad which were arranged in longitudinal rows with short spaces between. These cocoons, which were placed with the current, occurred on the wet walls of wooden chutes or runways and also on dripping chalk cliffs. The immature stages spend their existence in these small cocoons of mud and silk. When ready to emerge as an adult, the pupa makes its way thru the end of the cocoon away from the current, leaving the cast skin attached to the opening. The margins of the large pronotal breathing horns of the pupa are finely serrated and are presumably used in making this opening thru the cocoon. The young larva probably creeps about on the floor of the runway, feeding on algae growing in the same situation. When nearly full-grown, the larva crawls to a less exposed place and spins its cocoon. Many larvae and pupae are killed by the drying-out of their haunts when the water supply becomes insufficient to cover them.

Larva.— Length, 7 mm.
Diameter, 1.5 mm.

Body clearly depressed (Plate XXIII, 72), greenish white, scarcely shiny, with delicate appressed grayish hairs which are thicker at the two ends of the body, especially on last segment, where they become almost villous. Integument very transparent, so that intestine and contents show thru, the intestine narrowing on segment 6 and thru to segment 8, where it broadens out and almost entirely fills the ninth and tenth segments. On sides of prothorax a delicate, long, pale hair; on remaining segments two such hairs. On each of abdominal segments 3 to 9, on dorsum near anterior margin, a low transverse ridge which is thickly set with short, blackened points; on sternum of each of same segments, a similar welt which is destitute of points. In male larvae, clawlike appendages of genitalia of adults showing thru skin on ventral side.

Head capsule (Plate XXIII, 73 and 74) massive, slightly longer than broad, black, somewhat shiny, all the sclerites compact and closely united; anterior projecting part of capsule with margins transparent, rust-brown; median part with two small knobs, laterad of which are two larger projections which are crowned with short points; capsule weakly keeled behind on dorsum (Plate XXIII, 74), anterior to which are two swollen elevations; on hinder margin of clypeus a styliform, bristly lobe, easily broken off, which is presumably the antenna.

Labium strongly chitinized, triangular, split longitudinally. Mandible (Plate XXIII, 75) clawlike in appearance, a little smaller than either half of labium, on inner face with a chitinized projection which is serrated. Maxilla indistinct, the palpi coroniform. Spiracular disk (Plate XXIII, 77) with four lobes whose inner faces are narrowly lined with black chitin; lobes provided with lashes of long gray hairs; dorsal lobes the shorter and broader, and bearing on their inner face two elongated stigmata which are margined with pale rust-yellow.

Pupa.— Length, 6.5 mm.

Pronotal breathing horns (Plate XXIII, 76) large, ear-shaped; bright yellowish white in color, in contrast to dirty yellowish brown skin of head, thorax, and appendages; each horn consisting of two parts: the dorsal side, appearing smooth and homogeneous; and the ventral side, with two longitudinal furrows converging toward apices, and with abundant elongate tubercles, under low magnification this part appearing pitted because of the spaces between these tubercles. Margin of breathing horn chitinized and very finely notched. On outer basal part of each ear a parchment-like lobe, which joins ear to side of prothorax; in addition to this, each ear at base is drawn out into an almost rectangular lobe which is closely approximated to pronotum. Leg sheaths extending about to base of fifth abdominal segment. Abdomen distinctly depressed, greenish white in color; segments 3 to 7 on both dorsum and sternum near base with a double cross-row of spicules which present a comblike appearance (Plate XXIII, 78), those on dorsal segments being somewhat stronger. Female pupa with acidothecae grown together on inner face, at outer angle of each a chitinized hook which is curved upward. Male pupa with ventral side of last segment produced into two chitinized points which are bent toward each other and almost touch, these inclosing clasping organs of adult male and hooks of male larva as described above.

Subtribe **Limnobaria**

The subtribe Limnobaria includes about ten genera, which are very closely related to one another and whose limits are as yet not clearly defined. Many of the generic distinctions are based on male characters of wing form, venation, or antennal structure. The genera are often very large and it is difficult to give satisfactory characters to separate their immature stages. The keys to the genera, given below, will unquestionably need much revising when a larger number of forms are studied.

Larvae

1. Form stout; teeth of mandibles and of mentum usually more numerous; mentum more pointed anteriorly . . . . *Limnobia* Meig. (p. 809)
   Form usually more slender; teeth of mandibles and of mentum usually fewer; mentum transverse or subtransverse 2
2. Mandibles very broad, flattened, with three ventral cutting teeth; mentum about transverse, with nine or eleven teeth . . . . *Rhipidia* Meig. (p. 825)
   Mandibles more slender, with usually four or five cutting teeth; mentum usually a little pointed anteriorly, with about eleven teeth . . . . *Dicranomyia* Steph. (p. 819)

Pupae

1. The five basal abdominal segments on both dorsum and venter with a comb of small, blunt teeth; wing sheaths showing an ocellate pattern; pupae living beneath bark of coniferous trees .... *Discobola* O. S. (p. 815)
   Abdominal segments provided with basal transverse welts of microscopic points on segments 3 to 7; wing pattern not ocellate 2
2. Pronotal breathing horns long and narrow, about three times as long as broad. *Rhipidia* Meig. (p. 825)
   Pronotal breathing horns short and broad, length and breadth not greatly different.... 3
3. Size large (usually over 10 mm.); breathing horns often broader than long. *Limnobia* Meig. (p. 809)
   Size smaller (usually under 10 mm.); breathing horns usually as long as broad. *Dicranomyia* Steph. (p. 819)

Genus **Limnobia** Meigen (Gr. *swamp* + *I live*)

1800 *Amphinome* Meig. Nouv. Class. Mouch., p. 15 (*nomen nudum*, preoccupied in Annelida).
1803 *Limonia* Meig. Illiger's Mag., vol. 2, p. 262.
1818 *Limnobia* Meig. Syst. Beschr. Zweifl. Ins., vol. 1, p. 116.
1818 *Unomyia* Meig. Syst. Beschr. Zweifl. Ins., vol. 1, p. 116.
1856 *Limnomyza* Rond. Dipt. Ital. Prodr., vol. 1, p. 185.

Larva.— Form stout, terete. Abdominal segments with dorsal and ventral transverse welts covered with chitinized points on basal rings. Spiracular disk surrounded by indistinct lobes, the spiracles large. Head capsule large, massive, the dorsal plate narrowed behind and more or less bifid at its tip. Labrum transversely oval, with sensory bristles near margin. Mandible blunt, with from four to seven cutting teeth. Maxilla simple, cardo and stipes large. Antenna with apical papilla button-like. Mentum broad, margin with from eleven to thirteen teeth. Hypopharynx a circlet of two chitinized plates, each with from twelve to fifteen teeth.

Pupa.— No cephalic crest. Pronotal breathing horns flattened, earlike, as broad as, or broader than, long. Mesonotum unarmed. Abdomen with transverse welts of fine hooks on basal annuli of tergites 3 to 7 and sternites 5 to 7. Two tiny spiracles on dorsum of eighth abdominal segment.

Limnobia is a rather small genus (comprising about forty-five species) of usually large and handsome flies. The species are most numerous thruout the Holarctic and Ethiopian regions. The immature stages have a wide range of habitat.

Of the European species, *Limnobia bifasciata* Schr. [= *L. xanthoptera* Meig.] is characteristically fungicolous, the larvae occurring in various species of Agaricus and related genera as stated by Stannius, Pastejrík, De Meijere, and other investigators. *L. decemmaculata* Lw. occurs in fungi (Daedalea and similar species), as recorded by Loew (1873) and by Verrall (1912). *L. quadrimaculata* (Linn.) [= *L. annulus* Meig.] often occurs in tree fungi but is not confined to this habitat. This species,

L. macrostigma Schum., and *L. obscuricornis* Bel. are often found in decaying, principally deciduous, wood. *L. tripunctata* Fabr., *L. sexpunctata* Fabr. [= *L. nigropunctata* Schum.], *L. flavipes* Fabr., and *L. nubeculosa* Meig. are found in humous earth and beneath leaves in woods. The pupal duration of *L. quadrimaculata* is from eight to twelve days, and this species, as well as others of the genus, pupates in the ground, inclosed in delicate silken cases which are covered with particles of earth and other matter.

In America, *L. triocellata* O. S. is characteristically fungicolous. *L. cinctipes* Say, and presumably *L. immatura* O. S., are found both in fungi and in decaying wood. *L. indigena* O. S. has been found in living tulip roots from Greenville, South Carolina (Greene, ms.). *L. fallax* Johns., and presumably *L. solitaria* O. S., live in organic mud near water. *L. parietina* O. S. probably has a similar habitat, since it was found in tent traps set over Beaver Meadow Brook in the Adirondacks (Needham, 1908 a: 171).

Limnobia cinctipes Say

1823 *Limnobia cinctipes* Say. Journ. Acad. Nat. Sci. Phila., vol. 3, p. 21, no. 4.

Limnobia cinctipes is one of the largest and commonest American species of the genus Limnobia. It has been reared many times, some of the records being as follows:

On July 23, 1883, Pergande collected larvae in an old fungus growing on rotten wood. On July 20, 1886, the same species of larvae was found constructing silken cases thru the fungus, and later in the ground for pupation. The pupae were active, and were able to draw back and forth in their tubes. Adults began to issue on July 28, showing the pupal stage in this case to be not more than eight days.

On April 25, 1912, a number of specimens of this species were received from W. H. Shideler, of Miami University, Ohio. The specimens were taken at Oxford, Ohio, on April 20, when several hundred larvae and pupae were found in an old dry log. The young pupae in the wood are not covered with particles of débris, but the older pupae are inclosed in a case which is covered with wood fragments, only the top of the head and the tip of the abdomen projecting beyond the case. When the pupae are about to transform, the insect emerges to about half its length and the

skin splits down the dorsum, the pupal skin remaining in place after the adults have emerged.

On September 15, 1912, many full-grown larvae were found in a fleshy species of Fomes near Gloversville, New York, where they were associated with a much larger number of larvae of *Ula elegans* and a much lesser number of *Limnobia triocellata*. When about to pupate, the larva becomes pale green in color and incases itself completely in a silken sheath which is covered with particles of sand and other débris. As the pupa grows older, the case becomes harder and more rigid. Numerous little mites are to be found running up and down over these pupae, more especially at the head end, and possibly seeking ingress into the insect. One young pupa had a piece of cloth adhering to the side of its case. The pupal stage lasts about five days.

Larva.— Length, 18–22 mm.
Diameter, 2.5–3.2 mm.

Coloration light yellow to greenish, the setiferous transverse welts at base of abdominal segments brownish.

Body terete, abdominal segments subdivided into two narrow basal rings and a broad posterior ring. Abdominal segments 1 to 7 with a broad basal welt on tergites and sternites, that of the first segment much smaller; these welts densely covered with microscopic hooks; on the last two thoracic segments, welts indicated by very narrow lines. Cauda blunt, obliquely truncated. Spiracular disk (Plate XXIV, 83, and Plate XXV, 93) surrounded by indistinct lobes, the ventral margin projecting far caudad and indistinctly divided into two short lobes; lateral lobes very blunt; dorsal lobes short and blunt, often divided into two smaller lobes. Spiracles oblong or elliptical, placed obliquely. Gills four, blunt and rounded, formed for propulsion rather than for respiration.

Head capsule (Plate XXIV, 79) very much as in Antocha, the dorsal plate narrowed behind and somewhat bifid at apex; lateral plates shaped like a mussel shell, curved around to form mentum. Labrum (Plate XXV, 86) distinct, oval, the anterior margin fringed with delicate hairs, the hairs at the lateral margins longer and coarser; on either side near anterior margin, a blunt tubercle with three sensory bristles; just laterad of this a stout seta; along anterior margin, four sensory setae which are subequally spaced. Epipharynx densely hairy. Clypeus broader than labrum, with a seta at each outer anterior angle and two more on either side near posterior margin. Mentum (Plate XXIV, 81) elongate-triangular, not completely divided into halves but deeply split behind, with an outer plate running cephalad into a long, broad point; behind this another plate with the margins toothed, there being about five or six long, acute teeth on either side. Hypopharynx (Plate XXIV, 80) with two rows of teeth forming a circlet, into which duct of salivary gland opens; anterior row having about nine large, blunt teeth, with about six smaller teeth on either side, these latter sharper-pointed and more crowded; posterior row having long, pointed teeth, about twelve in number. Antenna (Plate XXIV, 82) two-segmented, the basal segment chitinized, elongate-

cylindrical, the second segment flattened, shaped somewhat like a door knob; a few sensory projections. Mandible (Plate XXV, 87 and 88) powerful, produced into a strong apical point, with about four or five blunt or irregular inner teeth and a strong dorsal tooth on outer margin before tip. Maxilla (Plate XXV, 87) large, the outer margin thickened, subchitinized; palpi at apex small, shaped like half a pill box, with a few sensory papillae at tip.

Pupa.— Length, 18–20 mm.
Width, d.–s., 2.8–3 mm.
Depth, d.–v., 3.1–3.3 mm.

Entire head and thorax, including leg and wing sheaths, light brown, the thoracic dorsum somewhat darker-colored, the wings more yellowish brown; abdomen pale light green, the segments with the submedian brown band interrupted on pleural region; tip of abdomen brownish, chitinized.

Form stout (Plate XXV, 89); body destitute of noticeable setae.

Head flattened (Plate XXIV, 84). Cephalic crest lacking; forehead with a shallow V-shaped notch between antennal bases. Eyes of male large, the front narrowed, with points of tentorium close to inner margin of eye; eyes of female more widely separated. Antenna rather short, ending just beyond wing root. Labrum short, obtuse. Labial lobes contiguous, divergent, blunt at their tips, posterior margin a little convex medially. Lobes of maxillary palpi large, subquadrate. Cheek with a large, flattened ledge overlying joint of fore legs.

Thorax very gibbous. A distinct anterior median carina between breathing horns. Pronotal breathing horns (Plate XXV, 90) flattened, earlike, broader than long, directed slightly proximad, margin with a row of breathing tubercles, outer face wrinkled. Wing sheaths reaching base of third abdominal segment. Leg sheaths reaching base of fourth abdominal segment or a little longer; tarsi ending about on a level, or sloping gradually from short hind tarsi to long fore tarsi.

Abdominal segments indistinctly subdivided into three rings; on tergites 3 to 7, and sternites 5 to 7, basal ring with a transverse welt which is densely covered with short hairs or hooks, these welts tapering gradually to ends; sternites of segments 3 and 4 having incomplete welts on either side of leg sheaths; band on tergum of segment 7 not broken medially, but a little constricted in some specimens; in older pupae the other annuli, especially the posterior one, variously darkened on dorsum and venter. Female cauda (Plate XXIV, 85) with the acidothecae short, the sternal valves the shortest, the tergal valves a little longer; prominent lateral lobes at base of tergal valves, and a slightly smaller but very broad one on each side of tergal valves at about midlength. Male cauda (Plate XXV, 91) similar to that of female, but the dorsal lobes (Plate XXV, 92) much shorter, not longer than the ventral lobes, and separated by a U-shaped notch; ventral lobes approximated, each ending in a small, blunt tubercle. Two small circular spiracles on dorsum of segment 8, these a little more widely separated in male than in female.

Nepionotype.— Gloversville, New York, October 26, 1912.

Neanotype.— Female pupa with type larva.

Paratypes.— Several larvae and pupae with types and from Oxford, Ohio, April 20, 1912.

Limnobia fallax Johns.

1909 *Limnobia fallax* Johns. Proc. Boston Soc. Nat. Hist., vol. 34, p. 125.

Limnobia fallax belongs to the *solitaria* group and is apparently more Austral in its distribution than the other members of this group (*L. solitaria* O. S., *L. hudsonica* O. S.).

Larvae and pupae were found by Dr. Johannsen near Ithaca, New York, July 20–26, 1905. They were wrapped in silken cases covered with earthy matter, and were removed from the soil near a brook.

Larva.— Length, contracted, 8–8.2 mm.
Diameter, 1.2–1.3 mm.

Coloration white.

Form stout and short, body terete. Transverse welts with chitinized points on abdominal segments 2 to 7, those on dorsal surface broad, those on ventral surface narrower. Spiracular disk blunt, surrounded by four indistinct lobes, the lateral pair the largest and capable of close approximation, closing the large yellow spiracles. Anal gills indistinct.

Head capsule of usual Limnobia type. Labrum (Plate XXVI, 95) broadly oval, lateral angles and disk of epipharynx with tufts of long hairs; anterior margin fringed with short setae; about eight sensory bristles and papillae along anterior margin. Mentum (Plate XXVI, 96) large, triangular, running out into a long median apical point; lateral margins with about six or seven flattened subacute teeth on each side. Hypopharynx as in this group: a collar formed of two chitinized, comblike plates; the first plate rectangular, its face covered with flattened scales, anterior margin with about fourteen acute pointed teeth, the two outermost much the smaller, acicular; the second plate a narrow band of chitin similarly toothed, the teeth at each end large, flattened, the next tooth very narrow, acicular, the remaining teeth, ten in number, flattened, acute, the middle teeth a little shorter and broader. Antenna (Plate XXVI, 97) with basal segment elongate, cylindrical, and apical papilla or segment very tiny, disklike. Mandible (Plate XXVI, 98) large, moderately broad, with apical tooth prominent, two large dorsal teeth, and a row of about five or six comblike teeth along ventral cutting edge, the most basal being short and blunt. Maxilla (Plate XXVI, 99) about as in this tribe, cardines and stipites large and simple; palpus large.

Pupa.— Length of cast pupal skin, 10–13 mm.

Labrum (Plate XXVI, 100) triangular, apex obtuse. Labial lobes prominent, subquadrate. Posterior margin convex medially. Pronotal breathing horns (Plate XXVI, 101) flattened, subcircular in outline, with an outer marginal row of breathing tubercles. Leg sheaths ending just before apex of fourth abdominal segment; tips of tarsi about on a level, or those of fore legs a little the longer. Band of spicules on seventh tergite, slightly constricted medially. Female cauda (Plate XXVI, 102 and 103) with tergal valves a little longer than sternal valves, and more acute at their tips; a small tubercle on outer margin of outer lobes before tips.

Nepionotype.— Ithaca, New York, July 21, 1905.
Neanotype.— Cast pupal skin with type larva.
Paratypes.— One larva and three pupal skins.

Limnobia triocellata O. S.

1859 *Limnobia triocellata* O. S. Proc. Acad. Nat. Sci. Phila., p. 216.

Limnobia triocellata is a common crane-fly in eastern North America. It is closely allied to the European *L. bifasciata* Schr., the immature stages of which have long been known.

Johnson (1906:2) found larvae of this species in a fungus at Riverside, Massachusetts, on August 21, 1904, which pupated on the 22d and emerged on the 30th and 31st, thus giving a pupal duration of about nine days. Malloch (1915–17 b:215–216) found larvae and cast pupal skins in an Agaricus at Urbana, Illinois, in September of 1915. The writer found larvae of *Limnobia triocellata* in a species of Fomes, associated with the larvae of *L. cinctipes* and *Ula elegans*, at Gloversville, New York, on September 15, 1912. C. H. Popenoe found larvae at Great Falls, Virginia, on September 8, 1912, in the fungi *Hypomyces Lactifluorum* (Schw.) Tul. and *Armillaria* sp., the adult flies emerging on October 7, 1912. Other specimens from the same place found on October 9, 1913, in a species of Clitocybe, produced adults on October 20. Scores of specimens were taken in *Boletus felleus* at Bradley Hill, Maryland, the flies emerging on July 16, 1914.

Larva.— Length, 10–18 mm.
Diameter, 1.2–1.4 mm.

Coloration a little more yellowish than that of *Limnobia fallax*. Species very close to *fallax* in all details. Ventral welt on abdominal segment 1 well developed, but dorsal welt lacking or very reduced. Spiracular disk (Plate XXVI, 94) rather large, exposed; circular spiracles large, separated by a distance less than the diameter of one; lobes surrounding disk small and indistinct.

Pupa.— Length, 12–15 mm. Not very different from other species of genus described herein.

Nepionotype.— Great Falls, Virginia, September 28, 1913.
Paratypes.— With the type.

Genus **Libnotes** Westwood (derivation obscure)

1876 *Libnotes* Westw. Trans. Ent. Soc. Lond., p. 505.

Libnotes is a small genus (about thirty-five species) of rather large crane-flies, which are chiefly Oriental in their distribution altho three species occur in South and Central Africa. The species *Libnotes perkinsi* (Grimsh.) has been considered as being a Limnobia, but it seems

to the writer that the present generic reference is more nearly correct, altho the distinctions between Limnobia and some species of Libnotes are very poorly marked. *L. perkinsi* was bred from larvae in damp moss (Perkins, 1913: clxxxii, as Limnobia), and in a letter to the writer Mr. O. H. Swezey states that he has reared this species from larvae in decaying vegetation and in the accumulation of débris behind old leaf-sheaths on banana plants (Musa, Scitamineae) in the Hawaiian Islands.

Genus **Discobola** Osten Sacken (Gr. *discus* + *I throw*)

1865 *Discobola* O. S. Proc. Ent. Soc. Phila., p. 226.
1869 *Trochobola* O. S. Mon. Dipt. N. Amer., part 4, p. 98.

Discobola is a well-marked genus including about eight described species, which are most numerous in the Australasian region, two species only being found in Europe and two others in America. The adults of the commoner American species, *D. argus* (Say), are not rare. They are most numerous in late summer, and are often found resting on the stumps and trunks of coniferous trees, especially white pine (*Pinus Strobus* Linn.).

The immature stages of *D. caesarea* (O. S.) were found by Mik (1884) in Austria, living in decaying pine stumps from which the bark had been removed. The following account is taken entirely from Mik's paper:

Male pupa.— Body cylindrical, slender (9.2 mm. long, 1.5 mm. in diameter). Head, prothorax, mesothorax, leg sheaths, and wing sheaths chitinized, dark brown, shiny, the last-named somewhat brighter than the others, the leg sheaths somewhat darker at their tips. Eyes kidney-shaped, strongly shiny, blackish, between them a small, triangular, blackish brown spot. Prothoracic breathing horns dull-colored, dark rust-brown at base, becoming a brighter rust-brown more distally, compressed laterally, tuberculate, with margin indented. Prothorax carinate, rust-yellow, margined on both sides by dull reddish brown tubercles. In fully colored specimens, forehead and leg sheaths blackish brown, wing pattern indicated on sheaths as somewhat diffused rings. Leg sheaths reaching end of abdominal segment 3, wing sheaths reaching end of abdominal segment 1. Metathorax and abdomen thin-skinned, the former verdigris-colored, the latter white or somewhat yellowish green; metathorax resembling an abdominal segment, but its posterior margin is unarmed, while the first to the fifth abdominal segments on both dorsum and venter bear a comb of very small, short, blunt teeth, which are closely approximated; these teeth chitinized and rusty brown at their tips, giving to abdomen the appearance of having brown incisions; these transverse rows of teeth interrupted at pleura. Sixth abdominal segment pale thruout and lacking the comb. Seventh segment shorter and narrowed on dorsum, pale, bearing on sternum a rust-yellow chitinized plate which is narrowed anteriorly, leaving an uncolored triangular area on either side at base of segment. Eighth segment swollen to include genitalia, the

two basal parts ellipsoidal, strongly shiny, rust-yellow, somewhat darker at tips, the apical parts small and knotlike, bluntly rounded; segment bearing on dorsum a weak triangular piece at its base; between apical parts of genitalia are inserted two small chitinized shields; on venter, between basal parts, sheath of penis is inserted.

Female pupa.— Body resembling that of male, but longer and somewhat stouter (length 10.5 mm., diameter 1.8 mm). Leg sheaths extending to just beyond midlength of abdominal segment 2. Seventh abdominal segment shortened and somewhat narrowed, on dorsum largely pale, with a narrow chitinized margin only on lateral parts, so that the unchitinized part forms a triangle with the apex directed backward; on sternum this segment almost completely chitinized, rust-yellow, only a small triangular area at base on either side remaining uncolored; chitinized plate separated from plate of next segment only by an incomplete segmentation, swollen, and bearing two longitudinal impressions. Eighth segment bearing on its dorsal surface the dorsal valves of ovipositor, fused at their base, chitinized thruout, rust-yellow in color; segment bearing on its ventral surface a depressed conical chitinized plate of a rust-yellow color, and with transverse impressed wrinkles; on either side a small, dark, chitinized, lower valve of ovipositor. Other characters as in male. (When the pupae are placed in alcohol, the green of the metathorax and the abdomen disappears and is replaced by a yellowish white color.)

Pupae were collected in large numbers in a pine wood near Hammern in Freistadt (upper Austria) in the latter days of August, 1882. The pupae live in pine stumps, near the ground, where the bark has been removed, more especially in situations where the wood is somewhat sappy and not yet completely decayed. Those found were not deep in the wood. Their presence was discovered by finding the teneral adults on and near a stump, and many cast skins of the pupae projecting horizontally, the caudal end of the body, up to the leg sheaths, adhering to the wood. No emergence holes were found on the cut surface of the stump. The adults at first have a very long, pale abdomen, which is of a verdigris color, most intensive at the base and paler toward the tip. The pupae that were found transformed as adults in from one to three days.

Genus **Geranomyia** Haliday (Gr. *crane* + *fly*)

1833 *Geranomyia* Hal. Ent. Mag., vol. 1, p. 154.
1835 *Limnobiorhynchus* Westw. Ann. Soc. Ent. France, vol. 4, p. 683 (spurious name).
1838 *Aporosa* Macq. Dipt. Exot., vol. 1, part 1, p. 62.
1865 *Plettusa* Phil. Verh. Zool.-Bot. Ges. Wien, vol. 15, p. 597.

Geranomyia is a rather extensive genus including about eighty species, which are most abundant in the tropics of America, Asia, and Australia. On the African continent the genus is apparently less common. The adult flies have an elongate rostrum which is used for sucking nectar

from tubular flowers. The various species of the genus have been recorded as feeding on a wide range of plant species, which have been indicated by Knab (1910) and by Alexander (1916 b:486–493) and may be summarized as follows:

Species	Plants frequented
Geranomyia canadensis	Compositae — Eupatorium, Solidago, Aster, Silphium, Rudbeckia, Verbesina, Cacalia, and similar species
Geranomyia diversa	Compositae — Solidago, Erigeron Umbelliferae — Daucus
Geranomyia virescens	Lauraceae — Persea
Geranomyia rostrata	Compositae — Eupatorium, Solidago, Helianthus

For many years nothing was known concerning the immature stages of any species of Geranomyia. In 1917, J. R. Malloch found larvae and pupae of *G. canadensis* at Urbana, Illinois. Mr. Malloch and the writer have in-press a detailed paper on the immature stages of this species, and the following brief account is abstracted from this paper and included herewith in order to complete the data.

Mr. Malloch found the larvae on the grounds of the Floriculture Department of the University of Illinois. There is a small bubbling fountain here, the waste water from which flows along an open gutter. In this gutter the immature stages of *G. canadensis* lived among the vegetable growth and diatomaceous ooze in the bottom of the trough. Mr. Malloch and the writer found this same species in Union County, southern Illinois, in 1919. Here larvae and pupae occurred on the face of rocks where the surface was continually damp with percolating water. A railroad bank had been formed by piling up slabs of limestone to a height of about four feet. In the irregularities and crevices of these pieces of limestone, the larvae of Geranomyia were living in delicate silken tubes covered with a deposit of silt and diatoms. They emerged from their cases to feed on the exposed surface of the wet rocks during twilight, and even during the hours of sunlight, but upon being disturbed or alarmed they retreated with great agility into their tubes. The pupae are found in short, nearly vertical burrows in the same situations as the larvae; here they rest with only the long, conspicuous breathing horns projecting from the entrance to the burrow. When transformation takes place, the pupal skin projects from the mouth of the burrow nearly to the ends

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of the wing sheaths. The number of larvae vastly exceeds the number of pupae, and this would seem to indicate that the pupal existence is of very short duration, else this stage would be found oftener.

Larva.— Length, 12–12.5 mm.
Diameter, 0.8–0.9 mm.

Coloration grayish subhyaline; a large orange area on posterior lateral parts of prothorax; abdominal welts dark brown.

Form moderately long and slender; thoracic segments gradually decreasing in length from prothorax to mesothorax; abdominal segments gradually elongated to the fifth, thence shortened to end of abdomen. Ventral surface of meso- and metathorax and of first eight abdominal segments provided with a basal transverse welt which is densely set with microscopic points; on dorsal surface these bands smaller, occurring on metathorax and on abdominal segments 2 to 8, not connected with sternal bands except on metathorax and on eighth abdominal segment. Spiracular disk similar to that in Dicranomyia; the usual ventral lobes represented only by two small, dusky, setiferous areas. Spiracles large, elongate-oval, placed obliquely on the sides of a deep split and so capable of close approximation. Anal gills four, each short, tapering gradually to the blunt tip.

Head capsule compact, massive, as in tribe. Labrum transversely oval, margin with short yellowish hairs and a larger tuft on either side. Antenna two-segmented, second segment rather stout, cylindrical, slightly arcuate; apical papilla small but high. Mandible broad and flattened, with a small dorsal tooth and a row of five ventral teeth. Maxilla generalized in structure, as in tribe. Hypopharynx as in Limnobaria, consisting of a roughly circular chitinized collar provided with a crown of stout teeth. Mentum broad, undivided, anterior margin with eleven teeth.

Pupa.— Length (including breathing horns), 8–9 mm.
Length of breathing horns, 1.2–1.3 mm.
Width of body, d.-s., 0.85–0.9 mm.
Depth, d.-s., 1–1.05 mm.

Pronotal breathing horns grayish subhyaline; head and thorax with sheaths dark brown; abdomen whitish, hooks and spines brown.

Cephalic crest small, indistinctly bilobed, not setiferous; front long and parallel; rostral sheath very long and narrow, subtended on either side by sheaths of paraglossae, the latter projecting beyond tip of rostrum and ending almost opposite end of wing sheath; margin of cheeks flattened as in Limnobaria. Antennal sheaths short, ending slightly beyond base of wing pad. Pronotal breathing horns very large and prominent, not contiguous basally; about a dozen breathing pores along dorsal margin. Mesonotum unarmed; wing sheaths ending opposite base of third abdominal segment; leg sheaths ending opposite or slightly beyond midlength of fourth abdominal segment; tarsal sheaths ending about on a level. Abdominal segments 3 to 7 near base with two bands of chitinized hooks arranged in curved transverse rows inclosing an oval transverse area. Cauda chitinized, tergal region produced into two parallel curved hooks bending strongly dorsad.

Found at Alto Pass, Union County, Illinois, June 6, 1919.

Genus **Dicranomyia** Stephens (Gr. *fork* + *fly*)

1818 *Furcomyia* Meig. Syst. Beschr. Zweifl. Ins., vol. 1, p. 106 (*nomen nudum*).
1829 *Dicranomyia* Steph. Cat. Brit. Ins., vol. 2, p. 243.
1830 *Siagona* Meig. Syst. Beschr. Zweifl. Ins., vol. 6, pl. 65, figs. 5–7.
1830 *Glochina* Meig. Syst. Beschr. Zweifl. Ins., vol. 6, p. 280.
1854 *Numantia* Bigot. Ann. Soc. Ent. France, ser. 3, vol. 2, p. 470.

Larva.— Form slender. Body nearly glabrous, abdominal and thoracic segments with dorsal and ventral transverse welts on basal annuli. Spiracular disk small, the five lobes indistinct but indicated, spiracles large. Anal gills four, slender. Head capsule massive, of the Limnobia type. Mouth parts almost as in Limnobia; ventral cutting edge of mandible with fewer teeth; mentum with anterior margin more transverse and with fewer teeth.

Pupa.— Cephalic crest lacking. Pronotal breathing horns broad, in *D. simulans* with a basal recurved hook on dorsal side, in other known species unarmed. Basal abdominal annuli with transverse welts. Dorsum of eighth abdominal segment with vestigial spiracles.

Dicranomyia is a very extensive genus including more than two hundred described species of usually small flies which are found in most parts of the world. The immature stages, which are found in a variety of habitats practically as extensive as is covered by the entire family of crane-flies, range from forms that are almost strictly aquatic, thru species living beneath the bark of trees, to still other species which are leaf miners.

In Europe, *Dicranomyia trinotata* (Meig.) is a characteristic member of the hygropetric association, the insects living on rocks in streams, where they are covered with a thin sheet of water and are usually associated with such insect forms as Beraea, Tinodes, Stactobia (Trichoptera), *Orphnephila testacea* (Ruthe), *Pericoma nubila* (Meig.), *Dixa maculata* Meig., *Oxycera pulchella* Meig., and other Diptera. The larva is cylindrical, measuring from 10 to 11 millimeters in length and from 1.5 to 2 millimeters in diameter. The dorsal surface is greenish mottled with darker, the ventral surface brighter. The larvae live in loosely spun silken cases in which they pupate. The pupae are about 10 millimeters long, and live in cocoons which are almost horizontal in position. The mature pupa breaks thru the cocoon by means of its sharp-edged breathing horns, the adult then creeping forth and leaving the cast pupal hull behind. (Thienemann, 1909:64–65, and Grünberg, 1910:29.)

Dicranomyia dumetorum Meig. lives in decaying, principally deciduous, wood. Winnertz (1853) found it in large numbers in a decaying beech tree, associated with *Bremia cilipes* (Winn.).

A species of crane-fly doubtfully referred to *Dicranomyia pilipennis* Egg. (Schubart, 1854) has been found in ditch water in Holland.

Dicranomyia umbrata de Meij., a Javan species, lives in the slimy green algae floating in stagnant, as well as flowing, water. The pupae live in cocoons in the algal sheath, with the cephalic end projecting. The larvae are from 10 to 12 millimeters in length, cylindrical, about 0.6 millimeter in diameter, and of a yellowish color. The head is almost entirely retractile. The body is almost smooth, having only an inconspicuous transverse welt on the second abdominal segment near the posterior margin. The caudal end is somewhat enlarged and is truncated behind. De Meijere (1916:197–198) supplies a good description of the structure of the larval head capsule.

Dicranomyia foliocuniculator Swez., of the Hawaiian Islands, is the only recorded leaf-mining crane-fly. It was found by Swezey mining in the leaves of a species of Cyrtandra (Gesneriaceae) in the island of Oahu. Pupation of the species takes place within the mines (Swezey, 1913 and 1915).

In North America a number of species are known. *Dicranomyia simulans* has been ably discussed by Needham (1908a:214–217) and later by Malloch (1915–17b [1917]). This species is, for the most part, a member of the hygropetric fauna, dwelling in usually lotic water where it is associated with a characteristic rapid-stream fauna. Other conditions under which the species is found are discussed later. *D. badia* and *D. stulta* live in and under saturated moss cushions. *D. macateei* Alex. has been bred from larvae in decaying wood (Dr. W. G. Dietz). *D. rara* O. S. has been bred from larvae in a rotten willow, the larvae being taken on Plummers Island, Maryland, by H. S. Barber on October 12, 1913, and emerging as adults on November 14.

Dicranomyia simulans (Walk.)

1848 *Limnobia simulans* Walk. List Dipt. Brit. Mus., vol. 1, p. 45.

The best account of the life history of the common and widespread *Dicranomyia simulans* is that by Needham (1908a:214–216), quoted below:

> It is abundant on the piers along the west shore of Lake Michigan. . . . This pier [at Lake Forest, Illinois] was built on heavy driven piling, covered outside with heavy plank. About three feet of surface was exposed above the water at its normal stage. The planks were old, and sheltered a scanty growth of short, stemmed mosses in the cracks, and bore

a heavy fringe of Cladophora and other algae just below the water line, with a film of " skin algae " extending a little higher.

All over the sides of the plank, in either sun or shade, the adult *simulans* could be seen throughout the summer months, sometimes in considerable numbers. I was first attracted to notice them by their habit of running rapidly sidewise along the pier, and their resemblance to harvestmen (Phalangidae). They run habitually sidewise, apparently rarely moving forward except to escape an obstruction, and very rarely appearing on the top of the pier. They rest in an inverted position on the under surface of the overhanging plank on the top of the pier. They stick to the surface so persistently that it is difficult to make one take flight; they may be driven all about on the surface, or poked with a stick; they can fly well enough when they will, but when induced to fly they settle again almost at once, and within a few feet of their starting place.

They are associated upon the piers with *Geranomyia canadensis* and with numerous midges and micro-caddis flies (Hydroptilidae) and a few larger caddis flies of the genus Hydropsyche.

Males are more in evidence, but probably not more abundant in fact. The females come out from their resting places only to lay their eggs, and are only to be seen when busily engaged in the performance of this task. They stand on tiptoe, with the long ovipositor held in vertical position at the tip of the deflexed abdomen, and they swing the body up and down in rapid shuttlelike vibration, freely rising and falling on the long and widely outspread legs. Thus the point of the ovipositor is driven against the wet surface of the plank, thrusting almost as rapidly as the needlebar of a sewing machine; it is moved about over the surface, as if searching for soft spots in the wood, and occasionally it makes a deeper thrust when a suitable place is found, and an egg is deposited.

The egg-laying process is often interrupted and is continuously interfered with by the too importunate males. When a male in running about on the plank comes upon a female ovipositing, he stands directly above her at the full upward stretch of his legs, while she goes right along with her work; but the instant she ceases her vibrating and lifts her ovipositor, he is ready with his forceps, upturned and outspread at the tip of his decurved abdomen, to seize her. Usually she does not want to be interrupted and moves away, while he tries to run parallel and maintain all the while his position of vantage above her. Often other males are encountered, and then the males engage in a rough and tumble fight. They push and shove each other in a most ludicrous manner, reminding one of pigs fighting, and often an encounter of this sort enables the female to escape and go on quietly with her work.

The males have well developed eyes, but their sight must be very poor; for, while always searching for females, they seem quite unable to find them by sight, often passing females at work within a distance of a few centimeters. But their tactile sense seems more acute. When a male in running to and fro had passed several times within six centimeters of a female without noticing her, was deflected from his course toward her by an obstruction I purposely placed in his way, he instantly sprang toward her upon the slightest contact, even of tips of tarsi, but was quite unheeding until this contact occurred. If it did not occur he would pass on, even by the narrowest margin.

All stages are found together on the piers. The eggs are laid in the soft spots in the old wood, where the surface of the pier is kept wet, but not continually covered by water, in the zone of the " skin algae." The larvae live exposed or thinly algae covered, and crawl about slowly over the wet surface. They are greenish in color and very inconspicuous. In a cavity among the stems of the dwarf mosses (*Bryum binum* Schoeb. var. *varium* Lindb. and *Amblystegium orthocladon* Lesq. and James) in a crevice at the upper limit of the wet area the larva spins about itself a sheet of tissue and fastens bits of moss stems and leaves to its outside, and transforms inside the tube thus formed into a pupa. The tube is longer than its body, and the pupa moves in or out at will, doubtless by the aid of the hooks at the ends of its body.

The following descriptions of the immature stages are adapted from those of Needham and Malloch:

Larva.— Length, 10–15 mm.
Diameter, 1.5–2 mm.

Coloration green, with distinct brown marks on dorsum and with an interrupted mid-dorsal row of alternating paler dots and crossmarks; dark area made up of closely placed spinous hairs, clear areas for the most part devoid of hairs.

Body cylindrical, abruptly tapering behind on last abdominal segment. Legs lacking, but a scurfy, pubescent creeping-fold on under surface of meso- and metathorax, a similar one on first abdominal segment, and much larger, transversely placed, fusiform creeping-ridges on ventral surface of abdominal segments 2 to 7, on anterior ring of each segment. Incisions between dorsal segments of abdomen margined with blackish spinules, which are slightly stronger than other hairs of dorsum. Spiracular disk vertically cleft, with sloping sides, folded together when under water, border of aperture fringed with short hairs and destitute of fleshy lobes. Spiracles oval. Anal gills four, fleshy.

Head large, similar in general appearance to that of Limnobia, entirely retractile within enlarged prothorax; head showing a broad, pale yellow, median band, sides black from base of antennae backward. Labrum transversely oval, with a margin of close-set, scurfy hairs; clypeus one-fourth broader than labrum, yellow, with parallel sides but emarginate on front for reception of labrum; three recurved, stout setae on lateral margin of clypeus on each side, one on each angle and two on disk. Mentum slightly convex in outline, median tooth much longer and stouter than first lateral, second and third laterals as large as median tooth. Antenna long, the shaft about three times as long as its greatest diameter. Maxillary palpi short and inconspicuous.

Pupa.— Length, 8–9 mm.
Diameter, 1.5 mm.

Body smooth and shiny, ends brownish. Front of thorax upcurved dorsally. Pronotal breathing horns broad, laterally flattened, obtuse at apex, each with a basal recurved, sharp hook on its dorsal side; breathing tubercles arranged in a semicircular row along obtuse tip of horns. Dorsum of thorax with a faint fretwork of raised lines on surface. Abdomen smooth, with transverse lines of scurfy pubescence, terminating in a pair of stout, sharply recurved hooks.

Malloch (1915–17 b, pl. 33, fig. 5) has figured the peculiar pronotal breathing horn of this species.

Dicranomyia stulta O. S.

1859 *Dicranomyia stulta* O. S. Proc. Acad. Nat. Sci. Phila., p. 210.

Adults of *Dicranomyia stulta* are often exceedingly abundant, flying about, or resting in close proximity to, rocky ledges or cliffs near streams. They are found commonly in June, associated with such crane-fly species

as *Geranomyia canadensis, Dactylolabis montana, Tipula ignobilis, T. apicalis*, and similar forms. The larvae live in and beneath the saturated cushions of moss (Amblystegium) that grow on the shale near the water's edge. The only associated crane-fly larvae found near Cascadilla Creek, Ithaca, New York, where this species is common, were *Tipula ignobilis*, the larvae of both species being exceedingly abundant.

Larva.— Length, 10–12.2 mm.
Diameter, 0.6–0.7 mm.

Color pale whitish with a green cast; transverse abdominal welts dark brown.

Form rather long and slender. In addition to dorsal and ventral welts on abdominal segments 2 to 8, a complete band at base of metathorax and ventral bands on mesothorax and first abdominal segment; ventral abdominal bands larger and more conspicuous than narrow dorsal welts. A few erect setae on body. Spiracular disk (Plate XXVII, 105) rather small, with a deep vertical split, the large ovate spiracles capable of close approximation; ventral lobes blunt, with a black spot on face, fringed with short black hairs and with two sensory setae; each blunt lateral lobe narrowly lined with a black crescent; dorsal lobes very small, dusky; spiracular disk fringed with short, dark hairs. Anal gills four, large and pale.

Head capsule as in tribe. Labrum (Plate XXVII, 106) subtriangular; anterior margin broad, nearly straight across, with a dense fringe of hairs which are coarser at ends of lobe; near anterior margin of labrum two oval, hyaline areas, each with three short papillae; a few sensory setae along anterior margin. Mentum (Plate XXVII, 107) broad, anterior outline triangular, running out into a rather long apical point, each side with about five teeth. Hypopharynx (Plate XXVII, 108) as in this group of genera, consisting of a collar of two chitinized combs, each with about ten sharp teeth. Antenna (Plate XXVII, 109) short, cylindrical, the apical papilla very small, reduced to a tiny disk. Mandible (Plate XXVII, 110) broad, flattened, with a blunt apical point which is only a little longer than the teeth on either side of it; ventral cutting edge with about five blunt teeth, which are gradually smaller from the outermost toward the base; inner face of mandible with a blunt prosthecal tooth and an oblique fringe of coarse setae. Maxilla (Plate XXVII, 111) with the cardines large, with about three setiferous punctures; stipites short, cylindrical; outer lobe fringed with long hairs and bearing the short, flattened, disklike palpus, which has five or six hyaline pegs; inner lobe smaller, with dense, short hairs and a few sensory organs.

Pupa.— Length, about 6 mm.

Labrum very obtusely rounded at apex, not bilobed. Labial lobes straight across or very slightly convex across posterior margin. Maxillary palpi narrowed toward tips (Plate XXVIII, 112). Pronotal breathing horns (Plate XXVIII, 113 and 114) elongate-oval, earlike, the ventral margin more bulging, the apex a little narrowed but obtuse; a row of breathing pores along outer margin, beginning on lateral face near dorsal margin, these few in number and widely separated, becoming more numerous toward apex of organ. Leg sheaths as usual in this group of genera, those of fore legs the longest, those of hind legs the shortest. Male cauda (Plate XXVIII, 115) with ventral lobes (Plate XXVIII, 116) large, bluntly rounded at tips; two small, brown, approximated tubercles at base of split on

ventral side; two blunt tubercles on dorsal surface near base and close to median line (Plate XXVIII, 117). Tergal lobes at outer angles of a flattened plate, very short, triangular, each with two small hairs on caudal face before tip.

Nepionotype.— Cascadilla Creek, Ithaca, New York, May 22, 1917.
Neanotype.— Type locality, June 6, 1917.
Paratypes.— Abundant larvae and pupae with types, May 22 to June 6, 1917.

Dicranomyia badia (Walk.)

1848 *Limnobia badia* Walk. List Dipt. Brit. Mus., vol. 1, p. 46.
1859 *Dicranomyia humidicola* O. S. Proc. Acad. Nat. Sci. Phila., p. 210.

Dicranomyia badia is a very common species thruout eastern North America, occurring in gorges and ravines and along streams. The adult flies may be found resting on perpendicular cliffs near these haunts. In a position of rest they have all six feet on the support, a very different resting position from that of the often-associated genera Oropeza and Dolichopeza.

The larvae, as is frequent in this genus, live in and beneath moss, especially saturated cushions of moss growing in or near the margins of streams. They are of a clear light pea-green color, and simulate the moss to an astonishing degree. The writer found these larvae in Needham's Glen, Ithaca, New York, on April 16, 1917, beneath wet cushions of *Amblystegium irriguum* (Hook. & Wils.) B. & S., a moss that covers all the rocks and stones near water. In these moss cushions the larvae were associated with tiny larvae of *Tipula ignobilis* and pupae of *T. collaris*. When ready to pupate, the larva spins a small, silken, silt-covered case, which is further protected by a covering of small pieces of moss stems adhering to its outside, this case being hung up in the moss cushion, with the cephalic end of the pupa projecting. The pupal duration is about seven days (April 21 to 28 in the cases observed). The dark-colored pupa, with its contrasting yellow breathing horns, is very handsome.

Larva.— Length, 10.5 mm.
Diameter, 0.6–0.65 mm.

Coloration light pea-green, abdominal welts brown; after death general color fading to very pale greenish white.

Form slender; body terete, dorsal and ventral transverse welts at base of abdominal segments conspicuous. Spiracular disk (Plate XXVII, 104) with lobes indistinct, suffused with dusky, lateral lobes very blunt; disk surrounded by a fringe of short, dark-colored hairs. Spiracles very large, ovate, dorsal ends close together. Anal gills long and slender, pale.

Head capsule and mouth parts similar to those of *D. stulta*, already described, judging from the scanty material of *D. badia* available for study.

Pupa.— Length, 8–8.5 mm.
Width, d.-s., 1.1 mm.
Depth, d.-v., 1.2 mm.

Head, thorax, and appendages dark brown; pronotal breathing horns light yellow; abdomen greenish, the cauda chitinized, light brown.

Labrum very broad, indistinctly bilobed at tip. Labial lobes large, broadly transverse, posterior margin almost straight across. Maxillary palpi broad, tips truncated (Plate XXIX, 119). Lateral margins of cheeks flattened into ledges.

Pronotal breathing horns large, flattened, in lateral outline (Plate XXIX, 118) subcircular or nearly so, with a row of rather widely separated breathing tubercles along margin; as viewed from above, horns directed proximad, so as to be contiguous at tips. A high median crest on mesonotum behind breathing horns. Wing sheaths ending before apex of abdominal segment 2. Leg sheaths ending far before apex of abdominal segment 4; as usual in this division, the hind legs a little the shortest, the fore legs a little the longest. Abdominal segments with a distinct basal welt which is thickly margined with microscopic curved hooks. Lateral spiracles distinct, but small and probably nonfunctional. Female cauda with sternal valves shorter than long tergal valves, the latter (Plate XXIX, 120) almost straight, each with a powerful, acute spine on lateral margin at about midlength, this directed dorsad. Near the margin of segment 8, on dorsum, a pair of rudimentary spiracles.

Nepionotype.— Needham's Glen, Ithaca, New York, April 16, 1917. (No. 5–1917.)
Neanotype.— Type locality, May 7, 1917.

Genus **Rhipidia** Meigen (Gr. *a fan*)

1818 *Rhipidia* Meig. Syst. Beschr. Zweifl. Ins., vol. 1, p. 153.
1911 *Ceratostephanus* Brun. Rec. Indian Mus., vol. 6, p. 271.

Larva.— Form rather stout, body terete. Abdominal sternites 1 to 7 and tergites 2 to 7 with narrow transverse basal welts of chitinized points. Spiracular disk with indistinct lobes. Head capsule massive, not unlike that of Dicranomyia. Labrum broadly transverse. Mandible very broad, flattened, with only three ventral cutting teeth. Maxilla of simple structure. Antenna with apical papilla or segment very flattened, disklike. Hypopharynx of two chitinized plates, each with about twelve comblike teeth. Mentum almost transverse across anterior margin, with from nine to eleven teeth, the outermost fused.

Pupa.— Pronotal breathing horns elongate for this subtribe, about three times as long as broad. Abdomen with transverse bands of spicules on tergites 3 to 7 and sternites 5 to 7, and on extreme lateral parts of sternites 3 and 4.

Rhipidia is a small to medium-sized genus (about thirty-five species) having its center of distribution in the American tropics, with some species occurring thruout temperate Europe and America and a less number in Africa and the Oriental region. The genus is based on a sexual char-

acter, the pectinate antennae of the male, and several of the species run inconveniently close to Dicranomyia.

The immature stages are spent beneath the bark of decaying trees or in decaying vegetable or animal matter. In Europe the genotype, *Rhipidia maculata* Meig., has been recorded as living in old cow-manure. Beling found the insects in such a situation, associated with the larvae of *Rhyphus punctatus* (Fabr.) (Beling, 1879:52–53) and a staphylinid beetle, *Platystethus morsitans* Payk. (Beling, 1873 b:592). *R. uniseriata* Schin. was found by Beling (1879:53–54) living in decaying beech wood, in company with larvae of *Xylota lenta* Meig. and *X. segnis* (Linn.) (Syrphidae) as well as with larvae of a tipuline crane-fly, Ctenophora. The larvae of this species, like those of *R. maculata,* live in thin silken cases, open at both ends and covered with particles of wood and other débris.

In America, besides *Rhipidia bryanti* (which is discussed in some detail) the following records of the immature stages are available: *Rhipidia maculata,* recorded in Europe as living in decaying organic matter, was found by Needham (1908 a:170, 204) in tent traps set over the bed of Beaver Meadow Brook in the Adirondacks, the insects presumably having emerged from the stream bed or from the thin layers of moss covering the exposed stones. *R. fidelis* O. S. was reared from larvae in decaying wood near Ithaca, New York, by Carl Ilg. This species belongs to the same subgenus (Monorhipidia Alex.) as the European *R. uniseriata,* which has similar larval habits. *R. domestica* O. S. has been bred from larvae obtained in fermented sap of the sour gum (*Nyssa sylvatica* Marsh., Cornaceae) at Clementon, New Jersey (Johnson, 1910:704). Males and females of this species were bred by Popenoe at Washington, D. C., from larvae on more or less decaying roots of taro (*Colocasia antiquorum* Schott, Araceae) taken at Gough, South Carolina, on February 1, 1911. Specimens of *R. domestica* emerged on August 21, 1906, at Juneau, Alaska, in radishes infested with *Hylemyia brassicae* (Bouché).

Rhipidia (*Rhipidia*) *bryanti* Johns.

1909 *Rhipidia bryanti* Johns. Proc. Boston Soc. Nat. Hist., vol. 34, p. 123–124, pl. 16, fig. 20.

Rhipidia bryanti is one of the largest and handsomest species of the genus, and is widely distributed thruout the eastern United States from Maine to Texas. The immature stages are spent beneath the decaying

bark of trees. The material studied was collected by J. R. Malloch in Potomac Park, Washington, D. C., on May 11, 1913, and was reared by R. C. Shannon (No. 35–1913), whose notes on the subject are as follows:

A small colony (about seven) of tipulids were found in a hollow of a tree behind the bark. The larvae were covered with slime, which gathered débris as they moved about and so formed a case. The next morning one had pupated. Two larvae were boiled and preserved in alcohol, while two others were preserved in formal. As they move about they leave a path of slime behind them. On May 14, the one that had pupated on the 12th emerged. On May 18 another imago issued.

There is an obvious error in the duration of the pupal stage as given — only two days. It is possible that a pupa was included in the material and was overlooked in its case of débris. The date of emergence of the second adult would show a pupal duration of six days, which is probably nearly correct.

Larva.— Length, 13.2–14 mm.
Diameter, 1 mm.

Coloration white.

Form terete, rather stout. Sternites 1 to 7 and tergites 2 to 7 with narrow transverse welts on basal rings; welts yellow, provided with long, transverse rows of microscopic roughened points, those along margins of welts coarser, those in centers very tiny; these rows interrupted along pleura. Caudal end blunt, with lobes of spiracular disk indistinct. Spiracles large, capable of close approximation.

Head capsule massive, of the Limnobia type. Labrum (Plate XXX, 121) broadly transverse, anterior margin almost straight across, near margin two oval areas which are provided with small sensory papillae. Epipharyngeal region with abundant hairs. Mentum (Plate XXX, 122) chitinized, the anterior margin almost transverse, with a large median tooth and about three lateral teeth on either side, the outermost of these an evident fusion of about three lesser teeth. Hypopharynx (Plate XXX, 123 and 124) as usual in this subtribe, a collar-like structure composed of two parallel combs united at the ends; the larger plate broadly elongate, surface with abundant scalelike plates, anterior margin with twelve teeth, the lateral ones narrow, the teeth gradually enlarging toward the middle, the middle pair a little shorter; second plate of hypopharynx broadly transverse, narrow, likewise with about twelve teeth, the two outer most on each side long, subacute, the middle tooth shorter and more flattened; between the two middle teeth a small triangular or conical point. Antenna (Plate XXX, 125) short cylindrical, the apical papilla a very flattened disk or button which is much broader than long. Mandible (Plate XXX, 126) very broad, flattened, with the apical tooth rather long and slender; two smaller teeth dorsad and three others ventrad, the dorsal teeth blunt, the ventral teeth truncated, the most basal tooth very broad. Maxilla (Plate XXX, 127) of the simple generalized structure of this tribe; cardines large, with two setiferous punctures; stipites weakly chitinized basally; outer lobe of maxilla with the large flattened palpus at its tips; palpus surrounded by numerous long setae and having several hyaline sense pegs at its apex; inner lobe of maxilla smaller, with numerous long hairs, especially a slitlike brush near margin.

Pupa.— Length, about 12 mm. (cast skin).

Labrum broad, rounded at apex. Labial lobes broadly transverse, caudal margin indistinctly trilobed. Maxillary palpi large, flattened, apex bluntly pointed; a rather angular tooth on margin near base (Plate XXXI, 128). Cheeks produced into flattened ledges. Antennae short and stout.

Pronotal breathing horns (Plate XXXI, 129) elongate for this subtribe, about three times as long as the greatest diameter, flattened, apical half slightly expanded, margin with tiny tubercles. Wing sheaths attaining base of abdominal segment 3. Leg sheaths attaining base of abdominal segment 5; tarsi ending about on a level, or hind tarsi a little the shorter and fore tarsi a little the longer. Abdomen with basal bands of setae on tergites 3 to 7 and sternites 5 to 7, and on the extreme lateral parts of sternites 3 and 4; these bands thickly margined with tiny, golden-yellow hairs or points, the median part of each band naked or nearly so. Male cauda (Plate XXXI, 130) with dorsal lobes (Plate XXXI, 131) very small, more or less flattened, divergent, rather blunt at tips; ventral lobes elongate, contiguous along inner face.

Nepionotype.— Potomac Park, D. C., May 11, 1913.
Neanotype.— Cast pupal skin, with type larva, May 14, 1913.
Paratype.— One larva with type.

Subtribe **Dicranoptycharia**

The subtribe Dicranoptycharia, so far as known, includes only the genus Dicranoptycha. The division is close to the Rhamphidaria but is easily separated from it in all stages.

Genus **Dicranoptycha** Osten Sacken (Gr. *fork* + *fold*)

1818 *Marginomyia* Meig. Syst. Beschr. Zweifl. Ins., vol. 1, p. 147 (*nomen nudum*).
1859 *Dicranoptycha* O. S. Proc. Acad. Nat. Sci. Phila., p. 217.

Larva.— Form very elongate, terete. Integument smooth, glassy, transparent. Abdominal segments 2 to 8 each with a basal transverse band or area of microscopic chitinized points on ventral surface; segment 8 with a similar band on dorsum. Spiracular disk surrounded by four lobes, the lateral pair more slender than the blunt ventral pair; dorsal lobe very low or lacking; a triangular brown mark on disk between spiracles. Spiracles small, widely separated. Anal gills a fleshy protuberant ring surrounding anus.

Head capsule compact, massive, the prefrons large with a few marginal punctures; externolateral plates very broad. Labrum large, flattened, pale. Antenna two-segmented; apical segment almost as long as basal segment, gradually narrowed to the blunt tip. Mandible with a blunt dorsal and two blunt ventral teeth. Maxilla generalized in structure. Hypopharynx a rounded cushion. Mentum deeply split behind but not completely divided, with three principal teeth and a small reduced lateral tooth on either side.

Pupa.— Cephalic crest low, depressed, setiferous. Labrum tumid. Labial lobes oval, contiguous. Antennal sheaths ending opposite base of wing pad. Pronotal breathing horns microscopic, represented only by tiny triangular tubercles. Mesonotum unarmed.

Wing sheaths ending opposite middle of third abdominal segment. Leg sheaths ending opposite base of fifth abdominal segment, the tarsi terminating on a level or nearly so. Abdominal tergites and sternites each with four transverse rows of microscopic setae; lateral spiracles on segments 2 to 7; no apparent spiracles on dorsum of segment 8.

Dicranoptycha is a principally Holarctic genus including twelve known species, six of which occur in the United States. The flies are of medium size and of a dull, inconspicuous appearance, and are rather difficult of taxonomic separation. The life histories of members of this genus have only recently been ascertained. The following notes are taken from more detailed accounts in earlier papers by the writer (Alexander, 1919, a and b).

The habits of the immature stages of Dicranoptycha may be briefly summarized as follows: The larvae and the pupae live in rich humous soil overlain with a cover of leaf mold and other vegetable débris. They frequent open woods where there is more or less shubbery and tall herbage. Running streams or rills are not necessary for the development of the immature stages. The larvae live in the uppermost zone of the soil, where they are associated with a rather characteristic group of animal forms, such as dipterous larvae (Sciara), beetle larvae, and centipedes. They are characterized by the exceedingly long, slender body and the shiny glabrous skin, and may be confused with no other dipterous larva yet made known. The glassy appearance of the body suggests the shiny shell of a small univalve snail, the dead fragments of which occurred in some numbers in the same situations. The larvae of *Dicranoptycha winnemana* Alex., an Austral species, attain a length of from 20 to 22 millimeters, with an average diameter of only 1 millimeter. The larvae of the genus are herbivores. When ready to pupate they incase themselves in compact earthen cells, which are 10 x 3.5 millimeters in size, firm in texture, and rather thick-walled but apparently without silk. There is a small opening at either end. The pupal period is about ten days or possibly a little less. Pupation takes place in the relatively dry soil that forms the larval haunt.

The pupa of *Dicranoptycha winnemana* measures from 9.1 to 12.8 millimeters in total length. The width at the wing pad is about 1.7 millimeters. The diagnostic features are given above at some length for the genus and need not be repeated here. For other notes the reader is referred to the papers already cited.

The adult flies of the various species of Dicranoptycha are usually abundant where they occur. They may be found resting on the upper surface of leaves of shrubbery and tall herbage in open woods, often far from water, which is not so necessary for development as with most species of Tipulidae.

Subtribe **Rhamphidaria**

The division Rhamphidaria includes the genus Rhamphidia, with the possible addition of a few exotic genera. Rhamphidia is one of the constituent genera of the former group Antochini, but differs considerably from all others whose life histories have been made known. The closest relatives of Rhamphidia seem to be the Dicranoptycharia, on the one hand, and the lowermost divisions of the Hexatomini, on the other. The larvae and the pupae of Rhamphidia present a curious eriopterine appearance, but their structure indicates only a distant relationship with the Eriopterini.

Genus **Rhamphidia** Meigen (Gr. *rostrum*)

1825 *Megarhina* St. Farg. et Serv. Encyclop. Method., Ins., vol. 10, part 2, p. 585.
1825 *Helius* St. Farg. et Serv. Encyclop. Method., Index, p. 831.
1829 *Leptorhina* Steph. Cat. Brit. Ins., vol. 2, p. 243.
1830 *Rhamphidia* Meig. Syst. Beschr. Zweifl. Ins., vol. 6, p. 281.

Larva.— Body terete. A transverse welt, covered with microscopic scabrous points, on ventral surface of basal annuli of abdominal segments 2 to 7. Spiracular disk surrounded by five short lobes which are fringed with abundant, rather long, hairs. Head capsule massive, generalized in structure. Mandible short and stout, ending in two subequal blunt teeth. Maxilla consisting of two rather short, densely hairy lobes. Antenna short. Hypopharynx chitinized, outer margin with about a dozen teeth. Mentum not completely divided, with five teeth. Coloration of body dark brown, produced by the dense appressed pubescence covering it.

Pupa.— Cephalic crest double, the anterior part low, the posterior part the larger; lobes setiferous, divergent. Two setae on front between eyes. Pronotal breathing horns long and slender, slightly curved. Mesonotum convex. Wing sheaths reaching end of second abdominal segment. Leg sheaths ending just before posterior margin of fourth abdominal segment; all the tarsi about equal in length, or those of fore legs a little longer. Abdominal segments with two narrow basal rings and a broader posterior ring having four narrow transverse bands of spicules and comparatively few setae. Spiracles rather large on pleurites 2 to 7, and a large conspicuous pair on dorsum of segment 8.

Rhamphidia is a small genus of crane-flies (about thirty-five species), widely distributed thruout the temperate and tropical regions of the world. The larvae of the European *R. longirostris* Meig. were found by Gercke

(1884) in submerged stems of the water dock, *Rumex aquaticus* Linn. The eggs are described as being rather long, white, and granulate. It is suggested that the developmental stages may be associated with water. The two local species have been reared and are discussed herewith.

Rhamphidia mainensis Alex.

1916 *Rhamphidia mainensis* Alex. Proc. Acad. Nat. Sci. Phila., p. 498–499, fig. 14.

Rhamphidia mainensis appears to be a rather uncommon form, much rarer than *R. flavipes*, the other local species. Adult flies were not uncommon in the Basin Swamp, Orono, Maine, on June 12, 1913. This swamp is a low, sunken area surrounded on most sides by hills, opening into the "Basin," an affluent of the Penobscot River. Cold springs of water percolate down from these hillsides, and the soil is very wet, boggy, and richly filled with organic matter. The chief floral constituents are a few elms and white birches and an abundance of alders, *Spiraea latifolia* Borkh., and *S. tomentosa* Linn. The herbage consists of ferns such as Onoclea and Osmunda, patches of Iris, *Impatiens biflora* Walt., and many rushes and sedges. Crane-flies associated with *R. mainensis* on the date mentioned included the following: *Dicranomyia haeretica*, *Epiphragma fascipennis*, *Pseudolimnophila luteipennis*, *P. inornata*, *Limnophila fasciolata*, *L. macrocera*, *Pilaria recondita*, *Ulomorpha pilosella*, *Tricyphona inconstans*, *Erioptera vespertina*, and *Tipula sulphurea*, also an abundance of *Ptychoptera rufocincta* and *Bittacomorpha clavipes*.

Larvae were first found on April 20, 1917, in the dark, cold swamp known as Larch Meadows, south of Ithaca, New York. Here they occurred in the thick, black, saturated organic matter comprising the soil of the swamp. The vegetation consists of the dominant alder (*Alnus incana* [Linn.] Moench.), the poison sumac (*Rhus Vernix* Linn.), and the marsh marigold (*Caltha palustris* Linn.), as well as an abundance of other plant species in lesser numbers. The earthy material in which the crane-fly larvae were found was full of the organic remains of plants, such as ferns, leaves, alder catkins, and the like. Associated with these larvae at this time were numerous small hydrophilid beetles, and a great abundance of larvae of a dascillid beetle of the subfamily Helodinae, of various sizes and ages. Numerous tabanid and stratiomyiid larvae, and the larvae of the crane-fly species *Bittacomorpha clavipes*, *Pseudolimnophila luteipennis*, and *Tipula dejecta*, also occurred.

The larvae were conspicuous by their dark coloration and, when placed in water, by their active, snakelike movements, in this regard being very different from somewhat similar larvae of certain Eriopterini which they resemble superficially because of the five subequal lobes surrounding the spiracular disk. The indoor pupal period is six days (May 8 to 14, 1917).

Larva.— Length, 9–11.2 mm.
Diameter, 0.75–0.9 mm.

Coloration dark brown, sutures pale; pale spots on dorsum and on sides of body; spiracular disk pale, lobes marked with darker.

Form rather stout, terete (Plate XXXI, 132). Body densely covered with a long, appressed, dark pubescence. Prothoracic segment narrowed in front, long, divided into two rings by a faint constriction; mesothoracic and metathoracic segments gradually longer. First abdominal segment shorter than last thoracic segment; abdominal segments 2 to 7 long, each divided into two narrow annuli by a deep constriction which is destitute of hairs but has just before it a sharp, transverse ridge of stiff hairs; short, incomplete ridges of these stiff hairs on dorsum of anterior ring; anterior ring about half as long as posterior ring; on ventral side of each of segments 2 to 7 on anterior ring, a transverse swelling, these swellings becoming more convex and prominent on posterior segments; swellings appearing almost smooth, being covered only with microscopic, roughened points; posterior ring with a sharp ridge of hairs at about two-thirds its length. Chaetotaxy as follows: dorsal segments with short setae at about midlength of posterior ring; a single rather stout, black bristle on pleura of anterior ring, immediately above transverse swellings; a similar seta on posterior ring; two groups of very long, delicate setae on ventral face of posterior ring, one on each side of the ridge of erect hairs; thoracic segments approximately similar to abdominal segments, but sternal setae at about midlength even more prominent. Last segment of body elongated, the spiracular disk (Plate XXXI, 136) surrounded by five lobes; dorsal lobe the smallest, rather blunt, inner face with a brownish, triangular-oval mark; lateral lobes of medium length, inner face suffused with brown, which is darkest, almost black, on lower edge of lobe; ventral lobes the longest, inner face of each with two broad, parallel, blackish lines, separated by a somewhat narrower pale line; entire disk fringed around with long, dark-colored hairs, which are longest near tips of lobes, where they are strongly recurved, almost pencil-like; fringe continuous between dorsal and lateral lobes, but between ventral and lateral lobes, and between the two ventral lobes, hairs toward base of each lobe very short to lacking; ventral lobes just before tips with a single long sensory bristle. Spiracles large, subcircular, situated at base of lateral lobes, dark-colored, narrowly margined with pale. Anal gills consisting of two pairs of pale, stout, cylindrical lobes, tapering toward tips, before which there is a slight constriction.

Head capsule massive and compact, of the normal generalized limnobiine type. Labrum large, conspicuous, transverse, densely fringed with long hairs; on epipharyngeal region, a large, dense tuft of moderately elongate hairs on either side of median line. Mentum (Plate XXXI, 133) not completely divided, but with a very deep split behind, a large median tooth, and two smaller teeth on either side; behind (dorsad of) elongate median tooth, a slightly wider flattened lobe whose margins extend beyond those of outer tooth. Hypo-

pharynx a broad semicircular band of chitin whose anterior margin is provided with about a dozen teeth, the intermediate ones more blunt and rounded, the lateral teeth longer and more slender. (The antennae of this species were not distinguishable in the specimens available, but are undoubtedly similar to those of *R. flavipes* described hereinafter.) Mandible (Plate XXXI, 135) of the generalized limnobiine type, short and stout, terminating in two blunt teeth; ventral cutting edge with about three teeth which are gradually smaller toward base of mandible; a dorsal row of two teeth, of which the basal one is the smaller; base of mandible on outer face (heel) prolonged into an acute flattened blade; a conspicuous tuft of hairs at prosthecal region. Maxilla consisting of two rather short, stout lobes which are shorter than the mandible, densely provided with short hairs; palpi large, shaped like a half of a short cylinder split lengthwise.

Pupa.— Very similar to that of *R. flavipes*, as described on the following pages. (The writer has only the cast pupal skin of *R. mainensis*, and it seems to agree very closely with the pupa of *R. flavipes* except that the lobes of the labial sheaths are longer and more pointed, and the labrum is a little longer to provide for the longer rostrum of the former species.)

Nepionotype.— Ithaca, New York, April 20, 1917.
Neanotype.— Cast pupal skin, May 14, 1917.

Rhamphidia flavipes Macq.

1855 *Rhamphidia flavipes* Macq. Dipt. Exot., 5th supp., p. 17.
1856 *Rhamphidia prominens* Walk. Ins. Saunders, vol. 1, Dipt., p. 435.
1859 *Rhamphidia brevirostris* O. S. Proc. Acad. Nat. Sci. Phila., p. 222.

Rhamphidia flavipes is a common and widely distributed fly thruout the eastern United States and Canada. The species is characteristic of cat-tail swamps and similar situations. It has been reared from leaves of bur reed, Sparganium, brought in by C. H. Kennedy from Ringwood Hollow, near Etna, New York, in September. These larvae were associated with larvae of *Prionocera fuscipennis*, likewise a characteristic inhabitant of open swamps. The specimens here described were taken in a small cat-tail swamp near Bool's hillside, Ithaca, New York, in June, 1917. Here they were associated with a number of larvae of characteristic swamp-inhabiting crane-flies, such as *Ptychoptera rufocincta, Pseudolimnophila luteipennis, Limnophila macrocera, Pilaria recondita, Liogma nodicornis* (in moss), *Prionocera fuscipennis*, and *Tipula tricolor*.

This is unquestionably the larva that was found by Hart and doubtfully referred by him to the genus Erioptera (Hart, 1898 [1895]: 197–199, also Malloch, 1915–17 b: 237). Later, Mik (1898: 62) doubted that this belonged to Erioptera because of the long lashes of hairs surrounding the caudal lobes, a character not shown by typical eriopterine larvae. The larvae that Hart found were living among rushes and other vegetation floating

on the surface of the water in the Illinois River. When submerged these larvae were very active, quite as noted in the account of *R. mainensis*.

Larva.— In all general features like larva of *R. mainensis* (with the material available the writer is unable to point out differences). Present species a little larger than *R. mainensis*, measuring from 12 to 13 mm. in length and 1 mm. in diameter. Mouth parts and head capsule almost exactly like those of *R. mainensis*, already described. Antenna (Plate XXXI, 134) with first segment elongate, a little enlarged toward tip, and with an elongate, thimble-shaped papilla at tip whose surface is delicately sculptured; surrounding this papilla at tip of basal segment, a few microscopic tubercles and pegs; on face of basal segment on proximal half, a circular porous plate.

Pupa.— Length, 7.8–8.8 mm.
Width, d.-s., 1 mm.
Depth, d.-v., 1.1–1.2 mm.

Coloration light brown; abdomen paler, trivittate with dark brown; a broad, dorso-median line, and narrower, somewhat interrupted, pleural stripes; breathing horns yellow, darker at extreme bases.

Cephalic crest (Plate XXXII, 137) low, the lobes divergent, their lateral angles with a stout seta which is directed cephalad. Just behind the anterior crest a much larger, low, appressed lobe, which is transversely wrinkled, bearing on its side a seta directed dorsad. Eyes rather large, widely separated by front; two setae on front between eyes. Labrum triangular, pointed at apex. Front a little elongated to provide for short rostrum of adult. Sheaths of maxillary palpi long, stout, almost straight. Labial palpi contiguous, lying side by side at tip of labrum. Antennae rather widely separated at their bases, ending just beyond wing root; in males lying across face of eye, due to the large size of eyes in this sex.

Mesonotum prominent, carinate medially (Plate XXXIII, 142). Breathing horns long and slender, slightly curved, transversely crenulated, a little enlarged toward tips; proximo-cephalad of base of each horn a small rounded tubercle bearing two setae. Lateral angles of thorax with about three short setae. Mesonotum convex, transversely wrinkled, with a few very short setae. Wing sheaths ending about opposite posterior margin of second abdominal segment. Leg sheaths parallel, about subequal in length or those of fore legs a little longer, ending just before posterior margin of fourth abdominal segment. Dorsal abdominal segments (Plate XXXIII, 143) each with two narrow basal rings and a much broader posterior ring; ventral segments (Plate XXXIII, 144) with the two basal rings confluent; dorsal segments with each narrow basal ring having a narrow, slightly arcuated band of spicules, and posterior ring having a narrow basal band of spicules which is more or less arcuated, and a straight caudal band, immediately in front of which are four groups of two setae each, or, in some specimens, with the intermediate groups reduced to a single seta; ventral segments with posterior ring having a broad transverse band of spicules, with three setae in alinement at each end of this band; closer to base of segment, two strong setae on either side; anterior ring darkened. Pleura with large but apparently nonfunctional spiracles on segments 2 to 7, a strong ante-spiracular seta, and three post-spiracular setae, as illustrated (Plate XXXIII, 144). Male cauda (Plate XXXII, 139 and 140) terminating in two acute tips which are directed dorsad; at base of these lobes on

dorsal face, two blunt, approximated, parallel lobes directed cephalad; at the base of long apical lobes, a shorter, pointed, setiferous lobe, directed laterad and dorsad, bearing on its side and near the apex a few setae. Dorsum of segment 8 with four prominent lobes surrounding a hollow, these lobes ending in acute tips, the posterior pair directed more dorsad, the anterior pair directed more laterad, at the base of the latter a pair of spiracles. Female cauda similar but with acidothecae prolonged, bearing on the side prominent lateral lobes (Plate XXXII, 141), corresponding to the setiferous lobe of male as described above; quadrangle of tubercles on dorsum of segment 8 (Plate XXXII, 138) about as in male, all the tubercles ending in chitinized points.

Nepionotype.— Ithaca, New York, May 11, 1917.
Neanotype.— Ithaca, New York, June 3, 1917.
Paratypes.— Pupae with neanotype.

Tribe **Hexatomini**

The tribe Hexatomini, as here understood, comprises a very extensive group of medium-sized crane-flies, made up of the members of the former groups Limnophilini and Hexatomini. The more generalized members of the group are herbivorous, but the two highest subtribes, Limnophilaria and Hexatomaria, are carnivorous in their feeding habits.

The larvae of the lower divisions have the head capsule massive and compact, the mentum chitinized and with the anterior margin toothed, and the hypopharynx usually well preserved. The mandibles are not formed into long, curved hooks, and the maxillae are of a generalized organization. The higher subtribes, Limnophilaria and Hexatomaria, have the head capsule long and slender and very much dissected, with the constituent plates very narrow and separate. The mentum is very reduced or lacking, in some of the Limnophilaria consisting of an articulated transverse bar which is grooved with parallel fine striae. In the group Ulomorphae and in the Hexatomaria the chitinized mental region is nearly, if not quite, lacking, allowing for great distention of this region of the head. The mandibles are powerful, curved hooks, bearing a few teeth at about midlength. In the group Ulomorphae the mandibles are hinged at about midlength, the basal part being deeply grooved on the inner face to receive the blade in a position of rest. The maxillae have the outer lobe prolonged into an elongate flattened blade which extends out of the thoracic orifice when the head is retracted.

The pupae of the Ularia and the Epiphragmaria have a pair of large spiracles on the dorsum of the eighth abdominal segment, indicating a close phylogenetic relationship with the Limnobiini. Dactylolabis has

the lateral abdominal spiracles protuberant, with those of the second segment very large and conspicuous. Pseudolimnophila, the Ulomorphae, and Pilaria have the pronotal breathing horns very long and slender, with the tips split into divergent flaps. In the Hexatomaria the lateral abdominal spiracles are large and functional.

The immature stages of the Polymeraria, including the single tropical American genus Polymera Wiedemann, are unknown. Their discovery might result in the inclusion of this subtribe with the Pediciini rather than with the Hexatomini.

The following keys separate the subtribes of the tribe Hexatomini:

Larvae

1. Mentum completely divided, each half with seven teeth on anterior margin; hypopharynx a semicircular chitinized ring with numerous teeth around anterior margin. *Pseudolimnophilaria* (p. 848)
   Mentum when present not divided; hypopharynx not shaped as above................2
2. Abdominal segments 2 to 7 with a basal transverse creeping-welt....................3
   Abdominal segments 2 to 7 without such a welt.................................4
3. Mentum three-toothed; antenna elongate, the apical segment hemispherical. *Epiphragmaria* (p. 843)
   Mentum nine-toothed; antenna short, subglobular, the apex with two short papillae. *Ularia* (p. 838)
4. Body depressed; head capsule massive, compact; mentum heavily chitinized, seven-toothed; maxilla not projecting.................................*Dactylolabaria* (p. 852)
   Body terete; head capsule of slender bars, not compact; mentum feeble, at most a narrow, transverse bar which is delicately striate; maxilla projecting from thoracic orifice.....5
5. Mental bar present.......................*Limnophilaria* (group *Limnophilae*) (p. 858)
   Mental bar lacking...6
6. Dorsal plates of head capsule firmly united; epipharynx and maxilla densely hairy; mandible hinged.......................*Limnophilaria* (group *Ulomorphae*) (p. 869)
   Dorsal plates of head capsule widely separated, at most merely contiguous behind; epipharynx and maxilla not hairy; mandible not hinged..........*Hexatomaria* (p. 876)

Pupae

1. Two large spiracles on dorsum of eighth abdominal segment..........................2
   No large spiracles as above...3
2. Pronotal breathing horns subchitinized, directed strongly ventrad; abdominal segments without shagreened transverse bands; pupates in wood........*Epiphragmaria* (p. 843)
   Pronotal breathing horns flattened, directed laterad; shagreened transverse bands on abdominal segments; pupates in earth.............................*Ularia* (p. 838)
3. Abdominal segments with large protuberant spiracles, those on second segment very large...*Dactylolabaria* (p. 852)
   Abdominal segments without conspicuous protuberant spiracles......................4
4. Pronotal breathing horns elongate, split into two flaps at tip.........................5
   Pronotal breathing horns not split into two such flaps..............................6
5. Abdominal segments with five or six rows of setiferous tubercles. *Pseudolimnophilaria* (p. 848)
   Abdominal segments without such rows of tubercles. *Limnophilaria* (group *Ulomorphae*) (p. 869)

6. Head and thorax without spines or tubercles; lateral abdominal spiracles small.
Limnophilaria (group *Limnophilae*) (p. 858)
Head and thorax often with tubercles on antennal scape, labrum, or mesonotal scutellum; lateral abdominal spiracles large, functional .... *Hexatomaria* (p. 876)

The most important literature on the tribe Hexatomini is as follows:

Ula macroptera	Larva	Stannius, 1829:205.
Ula macroptera	Larva, pupa, general	Perris, 1849:337–341.
Ula macroptera	General	Alexander, 1915 a:2.
Ula macroptera	General	Pierre, 1919–20:76.
Ula bolitophila	General	Loew, 1869:4–5.
Ula elegans	Larva, pupa, general	Alexander, 1915 a.
Ula elegans	Larva, pupa	Malloch, 1915–17 b:226. (Copy.)
Epiphragma picta	Larva	Bremi-Wolf, 1846.
Epiphragma picta	Larva, pupa	Beling, 1873 b:589–590.
Epiphragma fascipennis	Larva, pupa, general	Needham, 1903:281–285.
Epiphragma fascipennis	Larva, pupa	Malloch, 1915–17 b:224–225. (Copy.)
Pseudolimnophila luteipennis	Larva, pupa, general	Hart, 1898 [1895]:202–204.
Pseudolimnophila luteipennis	Larva, pupa, general	Malloch, 1915–17 b:222–223.
Dactylolabis wodzickii	Larva, pupa, general	Nowicki, 1867:340–343.
Dactylolabis denticulata	Larva, pupa, general	Mik, 1894.
Limnophila ferruginea	Larva, pupa, general	De Meijere, 1916:204–206.
Limnophila hyalipennis	Larva, pupa	Beling, 1886:198–199.
Limnophila lineola	Pupa	Beling, 1879:54.
Limnophila lineola	Larva	Beling, 1886:199–200.
Limnophila nemoralis	Larva, pupa	Beling, 1886:200–201.
Limnophila ochracea	General	Beling, 1886:202.
Limnophila pallida	Larva, pupa	Beling, 1873 a:556–558.
Limnophila dispar	Larva, general	Perris, 1849:331.
Limnophila pictipennis	Larva, pupa, general	Beling, 1879:51–52.
Limnophila pictipennis	Larva	Brauer, 1883:55.
Limnophila punctata	Larva	Scheffer, in Rossi, 1848:10.
Limnophila punctata	Larva	Osten Sacken, 1869:201.
Limnophila punctata	Larva, pupa, general	Beling, 1886:195–197.
Limnophila punctata	Larva	Gerbig, 1913:158–161.
Limnophila punctata	General	Cameron, 1917:63.
Limnophila bryobia	General	Mik, 1881:205–206.
Limnophila sinistra	Larva, pupa	Hudson, 1920:33–34.
Pilaria fuscipennis	Larva, pupa	Beling, 1886:197–198.
Pilaria fuscipennis	Larva	Gerbig, 1913:164–166.
Pilaria fuscipennis	General	Cameron, 1917:63.
Pilaria discicollis	Larva	Gerbig, 1913:163–164.
Pilaria discicollis	General	Cameron, 1917:63.
Pilaria tenuipes	Pupa	Hart, 1898 [1895]:204–205.
Pilaria tenuipes	Pupa	Malloch, 1915–17 b:223–224.
Eriocera spinosa	Larva, pupa, general	Alexander and Lloyd, 1914:27–30.
Eriocera spinosa	General	Alexander, 1915 c:149.
Eriocera cinerea	Larva	Alexander and Lloyd, 1914:21–23 (as *longicornis*).
Eriocera longicornis	Pupa, general	Alexander and Lloyd, 1914:23–27.

Eriocera longicornis	General	Alexander, 1915c: 149–152.
Eriocera fultonensis	Larva, pupa, general	Alexander and Lloyd, 1914: 30–33.
Hexatoma nigra	General	Von Röser, 1834.
Hexatoma megacera	Larva, pupa, general	Alexander, 1915c: 141–148.
Penthoptera albitarsis	Larva, pupa, general	Alexander, 1915c: 152–157.

Subtribe **Ularia**

The division Ularia includes only the genus Ula. It represents a very primitive group of crane-flies, presumably the most generalized of the entire tribe. The head capsule of the larva is oval and very massive, with the prefrons large and distinct. The head capsule and its arrangement of setae is not conspicuously unlike that of the eucephalous families of crane-flies, and this group of Tipulidae is presumably not very different from the early tipulid ancestors. The mentum is heavily chitinized, not completely divided behind, consisting of two plates, one behind the other. The outermost plate terminates in three teeth, while the second plate furnishes three additional teeth on each side. The hypopharynx is not chitinized. The antennae are very small; the basal segment is nearly globular, bearing at its tip two blunt, conical papillae. The mandibles are slender; the ventral cutting edge has about five narrow teeth; there is a distinct brush of hairs at the prosthecal region. The maxillae are of a generalized type, with the palpus large, flattened, and disklike. The abdomen is provided with six creeping-welts on the ventral surface of the segments. The spiracular disk is moderate in size, squarely truncated, surrounded by five subequal lobes which are heavily marked with black on their inner faces.

The pupa has the cephalic crest small and provided only with very small setae. The pronotal breathing horns are very long, tapering to the subacute tips. The abdominal segments have a basal transverse band of a shagreened appearance. The dorsal spiracles on the eighth abdominal segment are large and distinct.

The closest relative of the division is apparently the genus Epiphragma in the subtribe Epiphragmaria. But this entire group of genera (those included in the subtribes Ularia, Epiphragmaria, and Pseudolimnophilaria) is not far removed from the tribe Limnobiini.

Genus **Ula** Haliday (Gr. *soft*)

1833 *Ula* Hal. Ent. Mag., vol. 1, p. 153.
1864 *Macroptera* Lioy. Atti dell' Institut Veneto, ser. 3, vol. 9, p. 224.

Larva.— Body covered with a short pubescence. Basal annuli of abdominal segments 2 to 7 with a transverse creeping-welt on ventral surface. Spiracular disk squarely truncated, surrounded by five subequal lobes which are fringed with very short hairs. Head capsule massive, prefrontal sclerite very large, tapering to a point behind. Labrum large, conspicuous, with tufts of hairs. Mandible slender; ventral cutting edge with five teeth; a tuft of hairs on prosthecal region. Maxilla simple; palpus large. Antenna very small; basal segment subglobular, with two apical sensory papillae. Mentum not deeply divided behind; outer plate with three apical teeth; inner plate adding three additional teeth to each side. Hypopharynx not chitinized.

Pupa.— Cephalic crest small, setae tiny. Pronotal breathing horns long, tapering to subacute, flattened apices. Wing sheaths ending opposite base of third abdominal segment. Leg sheaths ending at about midlength of sixth abdominal segment. Abdominal segments on tergites and on apical sternites with transverse bands of microscopic points, producing a shagreened appearance; dorsal spiracles on segment 8 conspicuous.

The genus Ula includes only six described species, of which three are European, two are North American, and one is Javanese.

The adult flies of the American species are commonest in spring and late summer. They frequent cool, shaded gorges and ravines, or dark woods in mountainous regions, and may be swept from beds of low vegetation, such as ferns, yew, and other species.

The larvae of all the known species live in various species of fungi, but go to earth for pupation.

In Europe the common genotype, *Ula macroptera* (Macq.), has been discussed rather frequently in the literature. Stannius (1829:205) found the larvae in a species of Agaricus. Perris (1849:337–341) furnishes a brief account of the species, from which the following notes are taken: The fungus in which the larvae were found was *Hydnum erinaceum* Bull., growing on the trunks of living oak trees. The larvae are gregarious and frequent galleries in the fungus, along which they progress by means of their mandibles, by their ambulatory feet, and by the short hairs that cover the body. They were found in the month of November. A month later they went into the earth, where they transformed as pupae. The pupae bear a strong resemblance to those of Limnophila, but differ in the shape of the pronotal breathing horns. In February and March the pupae come to the surface of the earth and the adults emerge. The

caudal end of the larva is described as having but four lobes; no mention is made of the median dorsal lobe found in the American species, and it is presumably lacking or very reduced in size. Pierre (1919–20:76) has reared this species from larvae living in *Russula nigricans* Fries.

Another European species, *U. bolitophila* Loew, was bred from larvae living in fungi on beech trees in Austria (Loew, 1869:4–5).

In America, the immature stages of *Ula elegans* have been discussed by the writer (Alexander, 1915 a), the notes given below being in part supplementary to his earlier account.

Ula elegans O. S.

1869 *Ula elegans* O. S. Mon. Dipt. N. Amer., part 4, p. 276–277.

Ula elegans is a rather common species in mountainous regions thruout the northeastern United States. The adult flies swarm in early spring and again in the fall. At Ithaca, New York, on May 14, 1912, the writer found them swarming at half past four in the afternoon. There were about fifteen to twenty individuals in a swarm within a foot or two of the ground. In some cases the swarms were reduced to two or three individuals, or in a few instances to a single specimen. In copulation the flies rest on the upper surface of near-by plants (Symplocarpus, in the instance cited), with all the legs on the support. Copulation is rather firm, and the insects fly for short distances still united. The only crane-fly associated with Ula at that time was *Limnophila ultima* O. S.

On September 15, 1912, the writer found a fleshy species of fungus (Fomes) growing on a much-decayed stump close to the ground. This fungus contained a number of crane-fly larvae, including about thirty-five larvae of *Limnobia cinctipes*, a lesser number of *L. triocellata*, and many larvae of *Ula elegans*. The larvae of these species frequented the upper layers of the mushroom and had reduced the surface to a semi-liquid state. At the end of a week the whole fungus was reduced to a very decayed condition. The fungus, which was taken at Gloversville, New York, was then transferred to Ithaca, and was placed in large glass jars, with sand in the bottom to take up the liquids produced by decay and to provide a place for pupation. The first adults emerged on October 14. Emergence continued until the 27th, when the remaining pupae were killed and placed in alcohol. At that time they were very dark-

colored and evidently nearly ready to emerge to the adult state. At times the larval movements are very active and eel-like, but at other times they are very slow and sluggish. At each movement forward, the terminal segment partly telescopes into the subterminal and is thrown violently backward. After transforming to the adult condition, the pupal skin is left adhering to the sand, with the posterior half, or a smaller portion, attached, often standing quite perpendicular to the surface and very conspicuous.

Larva.— Length, 8.5–11.9 mm.
Diameter, 1.4–1.8 mm.

Color dull white; head capsule very dark brownish black.

Form moderately slender (Plate XXXIV, 145), but the body not greatly elongated as in the Eriopterini and some Limnobiini. Integument covered with a fine, short pubescence. Abdominal segments 2 to 7 each divided by a constriction into a narrow basal annulus and a broad posterior annulus; basal ring at about midlength and at the end with narrow transverse rows of tiny setae; abdominal segments 2 to 7 on ventral surface of basal ring with conspicuous raised transverse creeping-welts which are covered with microscopic points; eighth abdominal segment suddenly constricted before spiracular disk. Region around anus protuberant, this evidently being an aid to propulsion. Spiracular disk (Plate XXXIV, 153) surrounded by five blunt lobes, of which the dorsal one is median in position and blunter than the others; inner face of each lobe with a conspicuous brownish black mark; a fringe of delicate blackish hairs surrounding disk, these hairs a little longer and more prominent at ends of lobes. Spiracles almost circular, widely separated, the distance between them being about three times diameter of one spiracle. Disk between spiracles with an indistinct arcuated line.

Head capsule (Plate XXXIV, 146) massive and compact, rather narrow, posterior incisions not extending deeply into capsule. Prefrons very large, tapering gradually to a sharp point behind; numerous setae on prefrons and on other sclerites of capsule. Labrum (Plate XXXIV, 147) large, conspicuous; epipharynx and lateral margins strengthened by narrow bands of chitin; lateral and anterior margins of labrum with a dense fringe of long hairs; an irregular tubercle on dorsal surface on either side of labrum; epipharynx with a narrow transverse band of setae; juncture of clypeus and labrum with four setiferous punctures, two on either side, the posterior pair a little the closer together; clypeal region with a dark transverse basal and terminal band; base of clypeus with three setiferous punctures on either side. Mentum (Plate XXXIV, 148) almost completely undivided, the usual median split obliterated except behind; outermost mental plate terminating in three apical teeth, the median one of which is a little shorter and broader than the other two; behind (dorsad of) outer plate, another similar plate which adds three more teeth to each side of mentum. Hypopharynx not chitinized. Antenna (Plate XXXIV, 149) very small, short, cylindrical or subglobular, about as broad as long; at the tip two hyaline papillae shaped like immature mushrooms, the outer one about twice the size of the inner one. Mandible (Plate XXXIV, 150 and 151) slender, ending in a blunt, slightly curved, apical point; on ventral cutting edge a row of about five flattened

teeth; the more apical ones larger, the basal one very broad and truncated; two or three dorsal teeth, gradually lessening in size from tip of mandible toward base; two conspicuous tufts of long setae at prosthecal region; base of mandible on dorsal side with a large, somewhat curved, plate overlying head sclerites. Maxilla (Plate XXXIV, 152) with cardo long and narrow, transverse, with three conspicuous setiferous punctures bearing long setae; outer lobe short and stout, a little narrowed to tip; palpus rather large, flattened, disklike, the truncated apex with several tiny hyaline pegs; inner lobe with a sensory bristle and an inner fringe of rather short hairs.

Pupa.— Length, 6.4–7 mm.
Width, d.-s., 1.2–1.3 mm.
Depth, d.-v., 1.2–1.6 mm.

Mouth parts, wing sheaths, and leg sheaths rather dark brown; thoracic dorsum and abdomen light yellowish brown; pronotal breathing horns dark brown, passing into light yellow on apical third or quarter; mesonotal prescutum retaining its light color even in old pupae and those preserved in alcohol.

Cephalic crest (Plate XXXV, 155) represented only by a small bilobed protuberance behind and between antennal bases, each lobe tipped with a very tiny seta. Labrum short, bluntly rounded at tip. Labial lobes appearing as a large, roughly quadrate plate, a little narrowed behind and with all angles rounded. Sheaths of maxillary palpi very long and slender, rather stout at base, tapering to blunt tip. Antennae not conspicuous, rather widely separated at bases, ending just before or opposite origin of wing pad.

Pronotal breathing horns (Plate XXXV, 154 and 155) long and conspicuous, cylindrical, gradually tapering to subacute and flattened apices; horns directed laterad and cephalad, widely divergent. Thoracic dorsum without lobes or spines. Wing sheaths extending to just beyond end of second abdominal segment. Leg sheaths extending to about midlength of sixth abdominal segment; tarsal sheaths ending almost on a common level, the fore legs being a very little the longest, the middle legs a little shorter. Abdominal tergites with transverse rows of scattered punctures; on tergites 2 to 6 a transverse band of subchitinized points, producing a shagreened appearance; these bands located on basal rings of segments excepting the last two, which are on extreme ends of segments 5 and 6; on sternites the bands appearing only on segments 7 and 8, the other sternites being largely concealed by the unusually long leg sheaths; band on segment 8 very broad, but narrowly interrupted medially. Male cauda with ventral lobes bluntly rounded and inclosing pleural appendages of adult (in fully colored pupae these show thru the pupal skin as from twelve to fifteen strong, chitinized points on the inner posterior face); dorsal lobes (Plate XXXV, 157) very short and blunt, and closely approximated medially; on eighth tergite a broad rectangle of five lobes, including an anterior and a posterior lobe on either side and a much broader anterior median lobe; just proximad of anterior lateral lobes a large and distinct spiracle, in the cast skin with the large tracheal trunks still attached. Female cauda (Plate XXXV, 156) stout, tergal valves a little longer than sternal valves and a little upcurved.

Nepionotype.— Ithaca, New York, October 14, 1912.
Neanotype.— With type larva.
Paratypes.— Type locality, October 12 to 19, 1912.

Subtribe **Epiphragmaria**

So far as is known to the writer, the division Epiphragmaria includes only the genus Epiphragma. The immature stages are of a very primitive organization. The larvae have the head capsule broad and massive, with the posterior incisions very shallow. The labrum is broad, with lateral tufts of hair. The mentum is heavily chitinized, entire, with only a single lateral tooth on either side of the median tooth. The hypopharynx is not chitinized but the entire surface is provided with rows of tiny spinous points, somewhat as in the Dicranoptycharia. The antennae have the terminal papillae hemispherical. The mandibles are not greatly elongated; each has an apical tooth and two rows of lateral teeth. The maxillae are very simple in structure. The abdomen is provided with six ventral creeping-welts. The spiracular disk is large and simple, with the lobes short and obtuse.

The pupa has the breathing horns heavily chitinized, tapering to acute, slender points. The spiracles on the dorsum of the eighth abdominal segment are large and conspicuous.

The relationships of this group are obviously with the Rhamphidaria of the Limnobiini and the Ularia of the Hexatomini, the three groups probably being closer together phylogenetically than their arrangement in tribes would indicate. From a study of the adults alone, there seems to be little connection between the genera Rhamphidia, Epiphragma, and Ula, which were placed in three widely separated tribes by Osten Sacken. A study of the immature stages, the structure of the larval head, the abdominal creeping-welts, and the dorsal spiracles of the eighth abdominal segment of the pupa, indicate a relationship that cannot be denied.

Genus **Epiphragma** Osten Sacken (Gr. *upon* + *partition*)

1859 *Epiphragma* O. S. Proc. Acad. Nat. Sci. Phila., p. 238.

Larva.— Body nearly smooth; basal annuli of abdominal segments 2 to 7 with a naked transverse creeping-welt on ventral surface. Spiracular disk large, with four or five lobes, the dorso-median lobe often reduced. Spiracles large, circular. Anal gills four, retractile. Head capsule massive. Labrum broad, with lateral tufts of hairs and with two setae on anterior margin. Mandible with a blunt apical tooth and two rows of two lateral teeth. Maxilla small, simple; palpus large; inner lobe with a dense tuft of stiff hairs. Antenna two-segmented; basal segment elongate, apical papilla hemispherical. Hypopharynx not chitinized. Mentum entire, with only three teeth — a slender median tooth, and a broad, flat tooth on either side.

Pupa.— Cephalic crest erect, rectangular, the outer lateral angles produced into strong, chitinized spines. Pronotal breathing horns large at base, the elongate tips nearly chitinized, tapering into subacute points. Wing sheaths ending opposite base of third abdominal segment. Leg sheaths terminating just before end of fifth abdominal segment. Abdominal tergites with a transverse band of spicules at caudal margin; pleurites with a transverse oval area of similar spines; terminal sternites with a similar transverse band of spicules, most powerfully developed on segment 8; dorsal spiracles on segment 8 conspicuous.

Epiphragma is a rather small genus (twenty-five species) of usually large and handsome crane-flies, finding its center of distribution in the tropical regions of the New World. The adult flies of the local species are usually common. *Epiphragma fascipennis*, the best known of these species, is often found swarming in shady places, the swarms usually consisting of from twelve to fifteen individuals.

The immature stages of all the species thus far known are spent in decaying wood. In Europe, Beling (1873 b:589–590) records finding larvae and pupae of *E. picta* (Fabr.) in decaying ash (Fraxinus) and beech (Fagus) in the spring. He gives the pupal duration of this species as about two weeks. Needham (1903:281–285) gives an excellent account of *E. fascipennis*, which he found in partly decayed stems of willow and button-bush. The same species has been found living in the stems of black ash and elm. *E. solatrix* has been found in various deciduous trees in a dead or decaying condition. Bruch (*in litt.*) records an Argentinian Epiphragma from decaying wood.

Epiphragma solatrix (O. S.)

1859 *Limnophila* (*Epiphragma*) *solatrix* O. S. Proc. Acad. Nat. Sci. Phila., p. 238.

Epiphragma solatrix is a beautiful crane-fly, a little more Austral in its distribution than the more widely distributed *E. fascipennis*. H. S. Barber found larvae and young pupae very numerous in a drift log of sycamore (Platanus) at Plummers Island, Maryland, on May 19, 1913, and it is the study of this material that is included in this paper. Shannon found larvae in rotten wood at Rosslyn, Virginia, on November 23 and 25, 1912, and a pupa on January 3, 1913. Later he reared both *E. solatrix* and *E. fascipennis* from larvae taken from the same log on the same day. The species was again found in a decaying maple log on the Potomac River opposite Plummers Island, Maryland, where it was associ-

ated with the larvae of the syrphid fly, *Temnostoma bombylans* (Fabr.) and the supposed larva of Protoplasa (p. 770).

Larva.— Length, 18 mm.
Diameter, 1.6 mm.

Coloration pale whitish; anterior segments of body brighter-colored, more reddish.

Form stout and plump, not narrowed at ends of body. Pronotum longer than other thoracic segments. Integument covered with a short appressed pubescence. Abdominal segments 2 to 7 with conspicuous white creeping-welts on ventral surface of basal ring; these welts not interrupted medially, and entirely naked. Spiracular disk (Plate XXXVI, 163) large, unmarked, surrounded by five short lobes, the ventral pair very widely separated; dorsal lobe broad and obtuse; entire disk fringed with very short, delicate hairs which are interrupted only between paired lobes; inner face of lobes suffused with pale brown at tips. Spiracles large, circular, reddish with a very broad yellow margin, separated by a distance nearly equal to two times the diameter of one spiracle. Anal gills four, retractile.

Head capsule (Plate XXXVI, 158) broad and massive, the constituent plates firmly united except on ventral parts. Labrum broadly transverse; a median epipharyngeal part whose surface is finely pitted, bearing on ventral side near margin two stout setae; lateral angles of labrum directed proximad and densely tufted with hairs; extreme lateral margins of labrum with a curved hyaline seta; juncture of labrum and clypeus with two large setiferous punctures on either side; a few setiferous punctures on head capsule. Mentum (Plate XXXVI, 159) heavily chitinized, the outer face terminating in a single median tooth, behind which is a tridentate plate with three flattened teeth, the lateral ones very broad. Prementum (Plate XXXVI, 160) lying just behind mentum, a moderately broad transverse plate whose anterior margin is deeply and almost squarely notched, the lateral lobes thus formed being rounded or feebly indented at their tips. Hypopharynx (Plate XXXVI, 161) lying above and connected with prementum, consisting of a large flattened lobe, whose outer margin is evenly rounded, the surface densely set with longitudinal rows of small, subacute papillae. Antenna short, two-segmented; basal segment cylindrical, with auditory plate almost basal in position; apical segment small, subglobular or hemispherical. Mandible moderate in size, broad at base with a blunt apical tooth and a few blunt lateral teeth, two on dorsal cutting edge and two on ventral cutting edge, the more basal of these latter tending to be evanescent; two stiff setae at heel of mandible; a triangular lobe on dorsal face which projects onto lateral parts of labrum. Maxilla (Plate XXXVI, 162) primitive in structure; cardo elongate, transverse, with four setiferous punctures bearing powerful setae; outer lobe glabrous, with palpus at its tip; palpus slightly elongate, the auditory plate just before midlength; a seta on outer lobe below palpus; inner lobe of maxilla with a dense terminal brush of stiff yellow hairs and a few sensory papillae.

Pupa.— Length, 12–12.5 mm.
Width, d.-s., 2–2.1 mm.
Depth, d.-v., 2–2.1 mm.

Head, thorax, and appendages brown, becoming darker with age; pronotal breathing horns light red; abdomen whitish, the terminal rows of spicules on the segments chitinized.

(In older specimens the wing pattern shows on the sheath and is not distinctly fasciate as in *E. fascipennis*.)

Cephalic crest (Plate XXXVII, 166) erect, rectangular, the outer lateral angles directed ventrad and laterad as powerful chitinized spines, which in most cases curve outward; a stout seta beneath each spine. Labrum subtruncated or indistinctly bilobed at apex. Labial lobes triangular, projecting caudad as two cones. Maxillary palpi bent backward, lying along margin of cheek, stout, tapering suddenly to blunt tips. Cheeks projecting as flattened ledges. Antennae moderate in length, on scapal segment with a flattened tubercle on either side of cephalic crest; antennae extending rather far beyond wing root.

Pronotal breathing horns (Plate XXXVII, 164) with base enlarged, the elongate, subchitinized tips gradually narrowed, and the extreme apices subacute; breathing horns at tips directed ventrad and proximad; a truncated setiferous tubercle before each breathing horn. Mesonotum very deep. A short, but high, median crest behind breathing horns. Lateral angles of thorax produced into a slender lobe bearing a stout seta at tip. Wing sheaths ending opposite base of third abdominal segment. Leg sheaths terminating just before end of fifth abdominal segment; middle tarsal sheaths usually a little shorter than the others; in some specimens, especially females, fore legs the shortest, hind legs the longest. Abdominal segments (Plate XXXVII, 167) with two narrow basal rings and a broader posterior ring. Tergites on segments 2 to 7 near caudal margin of posterior ring with a narrow transverse crossband densely beset with acute spicules; on posterior segments these bands becoming gradually weaker, on segment 7 being very weak; two setae near lateral margin of posterior ring at about midlength. Pleurites with a transverse oval area with about twenty sharp spines near caudal margins of segments; a stout seta lying cephalad of this area. Spiracles distinct, oval, lying on ventral cephalic part of pleural posterior ring; a seta near dorsal margin of second basal ring. Sternites with a transverse band of spicules on segments 5 to 8, these being weakest on segment 5 at ends of tarsal sheaths and very strong and powerful on segment 8, where the band is interrupted medially; band often rather narrow but sometimes much broader. A seta near midlength of posterior ring on either side. Male cauda (Plate XXXVIII, 170) with dorsal lobes very stout, globose at base but soon narrowed into slender cylindrical appendages, each bearing three setae at tip; viewed from above, these lobes are seen to be separated by a wide U-shaped notch; ventral lobes blunt and with a flattened depressed disk at base of incision; eighth segment with a wide rectangle of lobes, two posterior lobes that are weakly setiferous and two smaller anterior lobes with a large spiracle proximad of each. Female cauda (Plate XXXVIII, 171) with tergal valves a little longer than sternal valves, upcurved, and with a stout seta before tip.

Nepionotype.— Plummers Island, Maryland, May 19, 1913.
Neanotype.— With type.
Paratypes.— Larvae and pupae with type.

Epiphragma fascipennis (Say)

1823 *Limnobia fascipennis* Say. Journ. Acad. Nat. Sci. Phila., vol. 3, p. 19.
1859 *Limnophila* (*Epiphragma*) *pavonina* O. S. Proc. Acad. Nat. Sci. Phila., p. 239.
1869 *Epiphragma fascipennis* O. S. Mon. Dipt. N. Amer., part 4, p. 194.

Epiphragma fascipennis is a very common crane-fly thruout eastern North America. As already stated, the immature stages are spent in decaying or partly sound wood, a wide variety of deciduous trees and shrubs being chosen, such as willow, elm, ash, buttonbush, and others. Needham gives the pupal duration as about twelve days, larvae and pupae found on May 18 emerging as adults on the 30th. A fully grown larva that the writer found in a decayed log beneath moss at Ithaca, New York, on May 8, 1917, pupated early in the morning of the 10th. The specimen died on the 18th, when about to emerge, and this would give a much shorter pupal period than is generally recorded for the genus. It was noted at the same time that the larva superficially resembles the larva of the leptid fly *Chrysopila thoracica* (Fabr.), with which it was associated but from which it is easily distinguished by its massive head capsule.

Needham found abundant pupae in a decaying log of black ash (Fraxinus) near Freeville, New York, on May 6, 1915. The pupae occurred in burrows in the semi-decayed wood. Adults emerged on the 11th. Additional material was found at Mud Creek, near Freeville, on May 15, 1915, in elm (Ulmus).

The account of the habits of the larvae as observed in Illinois by Needham (1903:281–285) is here quoted in part:

> The larvae bore in the dead and fallen stems of buttonbush and willow, where these lie on the mud at the borders of shallow ponds. I found them always in stems that were still partially sound, tunneling beneath the bark or even into the deeper parts and into the sounder wood. These stems are frequently submerged in spring and autumn, and even in summer, when the pond has gone dry, they are always saturated with moisture. . . . .
>
> The most interesting thing about the larva, aside from its wood-boring habits, is its singular adaptation to amphibian life. It must needs live part of the time wholly submerged beneath the waters of the pond, and part of the time out on land; it has, therefore, both open spiracles and tracheal gills; and, moreover, its tracheal gills are so placed that they may be withdrawn into the body in a dry time, where they escape the ills of too rapid evaporation.

In his description of the immature stages, Needham points out a probable error of Beling in describing a sexual dimorphism in the larvae of a species of this genus — Beling stating that the larvae producing females have three caudal lobes while those producing males have five. Malloch (1915–17b:224–225) cites Needham's descriptions of this species.

Larva.— (No larvae are available to the writer for a comparison with this stage of *Epiphragma solatrix*, but from Needham's characterization, and manuscript notes on specimens taken at Ithaca, New York, by the writer, the following differences seem to hold):

Spiracular disk surrounded by but four lobes, the dorso-median lobe being very reduced; inner faces of these lobes, as well as disk itself, entirely unmarked with darker.

Pupa.— Similar to pupa of *Epiphragma solatrix*, but differing as follows:

Cephalic crest (Plate XXXVII, 165) low, the lateral horns shorter, not elevated, and directed ventrad or slightly downward; setae on lateral face of spines often projecting above (cephalad of) it. Pronotal breathing horns shorter and stouter than in *solatrix*. Spines on eighth abdominal sternite widely separated or interrupted on median line. Male cauda (Plate XXXVIII, 169) with dorsal lobes much stouter than in *solatrix*.

Neanotype.— Bool's hillside, Ithaca, New York, May 8, 1917.
Paratype.— Pupa, Mud Creek, Freeville, New York, May 15, 1915.

The type pupa has one of the pronotal breathing horns deformed and bent caudad so as to be appressed against the body. Needham, who has a very much larger series available for study, notes this same peculiarity when he states that "a crumpled horn on one side is of rather common occurrence" (Needham, 1903:284).

Subtribe **Pseudolimnophilaria**

As at present constituted, the division Pseudolimnophilaria includes the single genus Pseudolimnophila, but other groups may be added to it when the immature stages of other species of the old genus Limnophila are made known. The larva is of a distinctly primitive type, the head capsule being compact and massive, the mentum chitinized and completely divided, each half provided with seven or eight teeth. The hypopharynx is a heavily chitinized semicircle with numerous teeth around the anterior margin. The antennae bear two elongate apical papillae. The mandibles each have two blunt apical teeth and two rows of lateral teeth.

The pupa is similar to that of the Limnophilaria, but the abdominal segments have transverse rows of setiferous tubercles.

The larva shows many points of resemblance to the tribe Limnobiini, and the two groups are probably derivable from an immediate common ancestor.

Genus **Pseudolimnophila** Alexander (Gr. *false* + *Limnophila*)

1919 *Pseudolimnophila* Alex. Cornell Univ. Agr. Exp. Sta., Mem. 25, p. 917.

Larva.— Body covered with delicate appressed hairs and numerous erect setae. Spiracular disk surrounded by four lobes, the ventral pair very long and narrow, with long fringes of hair. Gills four, long and slender. Head capsule massive, the sclerites large, fused.

Mandible short and blunt, of the generalized limnobiine type, the two apical teeth blunt. Maxilla not greatly projecting. Antenna slender, with two elongate apical papillae. Hypopharynx a chitinized band, with numerous teeth along anterior margin. Mentum completely divided, each half with about seven teeth.

Pupa.— Cephalic crest tipped with long setae. Pronotal breathing horns elongate, tips deeply split into divergent flaps. Abdominal segments with transverse rows of setiferous tubercles, there being five such rows on the tergites and six on the sternites. Lateral spiracles protuberant.

The name *Pseudolimnophila* was proposed for a certain group of the old genus Limnophila, including *L. luteipennis* and its allies. The adult flies closely resemble species of Limnophila, but the immature stages are very different and of a distinctly more generalized type.

The larvae are herbivores, with the mentum heavily chitinized, completely divided into two halves, the margin conspicuously toothed, the hypopharynx heavily chitinized and with numerous teeth, and the mandibles short and blunt and with many obtuse teeth. The points of resemblance to the Limnobia type are numerous, and the head capsule shows few features in common with Limnophila, in the restricted sense. The pupae have the abdomen with numerous transverse rows of setiferous tubercles bearing long setae. The genotype is *Limnophila luteipennis* O. S., of eastern North America. Other species referable to this genus are *L. inornata*, *L. contempta*, *L. nigripleura*, and *L. noveboracensis*, of the Nearctic fauna; *L. lucorum* (Meig.), of Europe; and *L. frugi* Bergr., *L. claduroneura* Speis., *L. natalensis* Alex., *L. spectabilis* Alex., and several other species, of the Ethiopian fauna.

Hart (1898 [1895]:202–204) describes the habits of *P. luteipennis* in some detail. Larvae about half grown were found on March 17, 1895, these attaining their growth and pupating on April 13. Hart ascertained by dissection that the species is a herbivore, feeding on fragments of dead vegetation, numerous diatoms of many species, and minute algae.

As in many species of the Limnophilaria and a few other groups of crane-flies, the spiracular lobes are fringed with long, delicate hairs which spread out on the surface film of the water into broad fans. The larva is unable to release itself from the hold of the water except by looping the head and the anterior end of the body around the posterior end, and drawing the latter thru this loop, repeating this action until the hairs have gone below the level of the film.

It is probable that other groups of species of the old genus Limnophila will be found to deviate from the characters of this group as now restricted. Species such as *L. hyalipennis* (Zett.), *L. nemoralis* (Meig.), and others in Europe, and *L. brevifurca, L. emmelina, L. mundoides, L. toxoneura, L. ultima,* and similar anomalous forms in America, should be investigated critically when opportunity offers.

Pseudolimnophila luteipennis (O. S.)

1859 *Limnophila luteipennis* O. S. Proc. Acad. Nat. Sci. Phila., p. 236.

Pseudolimnophila luteipennis is one of the most abundant species of the tribe, and is very widely distributed thruout eastern North America. The adult flies are common in swamps and along the marshy edges of streams and ponds. The immature stages are characteristic swamp inhabitants. They have been described in detail by Hart (1898 [1895]: 202–204). Malloch (1915–17 b:222–223) adds several supplementary notes and figures of Hart's material.

Larva.— Length, 15–18 mm.
Diameter, 1.5–1.7 mm.

Coloration light brownish yellow, slightly darker toward posterior end of body.

Body covered with a delicate appressed brownish pubescence and abundant stiff bristles and erect hairs on each segment, arranged in about five transverse rows; these bristles more numerous, coarser, and blacker, on posterior segments, forming a large tuft on sides of penultimate segment of body. Spiracular disk (Plate XXXIX, 176) surrounded by four lobes, the posterior pair very long and slender, finger-like, the lateral pair much shorter but slender; the inner face of these lobes with brownish black or dark brown transverse lines which cover almost the entire face; an arcuate line extending from ends of ventral marks across disk between spiracles; two small triangular marks located between ventral lobes; lobes fringed with long, delicate hairs, those at ends very elongate, those toward base of lobes shortened but continuous around disk. Anal gills four, very long and slender, exceeding ventral lobes of spiracular disk.

Head capsule short and stout, exhibiting a very generalized condition. Prefrons very broad, only slightly narrowed behind and but slightly exceeding lateral plates. Labrum broadly transverse, with a large tuft of hairs on either side. Mentum (Plate XXXIX, 172) completely divided, each half with seven (or rarely eight) teeth along anterior margin, of which the third (or fourth) from the inside is the largest; a flattened lobe just laterad of each half of mentum; mental plates continuous behind with strong lateral plates of capsule; in a normal position the two halves of mentum overlying each other to a greater or less degree. Hypopharynx (Plate XXXIX, 173) with anterior margin broadly rounded, with numerous (from ten to fifteen) bluntly rounded teeth. Antenna slender, with two long apical papillae. Mandible (Plate XXXIX, 175) short and broad, of the generalized limnobiine

type; tips blunt, ending in two large approximated teeth, with a row of smaller lateral teeth extending basad of each; ventral cutting edge with about four such lateral teeth, dorsal edge with one or two much larger teeth; two strong setae near base of scrobe, and two others near tip of mandible; a large brush of hairs at prosthecal region. Maxilla not projecting, with dense brushes of short, stiff hairs and with two short sensory tubercles which are tipped with very elongate setae; palpi stout and chitinized at base, the apex narrowed and pale.

Pupa.— Length, 10–13 mm.
Width, d.-s., about 1.5 mm.

Thorax reddish brown to black in color, depending on age of specimen; abdomen dirty whitish with narrow transverse brownish lines, both above and below; pronotal breathing horns dark brown or blackish.

Form subcylindrical, abdomen slightly depressed. Cephalic crest of two slender tubercles behind, tipped with long setae; another pair of setae between antennal bases. Pronotal breathing horns elongate, transversely ringed, the tips widely and deeply split into two divergent flaps. Prothorax with a prominent median carina. A tubercle in front of each breathing horn, each with about four stout setae. Mesonotum above wing axil with a tubercle bearing three setae. Wings reaching end of second abdominal segment. Legs reaching end of third abdominal segment, the tarsi ending about on a level or those of fore legs a little longer than those of other two pairs.

Abdominal segments divided into two annuli, the basal one still further subdivided into annulets; on tergum three annulets, each bearing a transverse row of setiferous tubercles, the setae very long and conspicuous, in some cases the tubercles multisetose, third annulet with two widely separated, slender, elongate tubercles. Posterior annulus with a basal and a terminal transverse row of setiferous tubercles. On sternum, four transverse rows of setiferous tubercles on basal ring and two on posterior ring. On pleura, protuberant spiracles. Lateral angles of segment 8 jutting out into stout lobes which are densely studded with setiferous tubercles, on ventral face continued toward median line as a nearly straight row of about eight setiferous tubercles, on dorsum a finger-like lobe on either side: Male cauda (Plate XL, 178) with sternal valves shorter than dorsal lobes, blunt at tips; tergal valves acutely pointed, directed dorsad. Female cauda (Plate XL, 179 and 180) with tergal valves considerably longer than the more slender sternal valves, broad medially, tapering to the broad, blunt tips which terminate in blackened points; two setae on outer margin.

Nepionotype.— Larch Meadows, Ithaca, New York, April 20, 1917.
Neanotype.— Female pupa, with type. No. 19–1917.
Paratypes.— Larvae with type. Pupae of both sexes from Bool's hillside, Ithaca, New York, June 6, 1917. A female pupa, Orono, Maine, taken as a larva June 13, 1913, emerged June 22. Female pupa, July 15, 1913, No. 75–1913.

Pseudolimnophila inornata (O. S.)

1869 *Limnophila inornata* O. S. Mon. Dipt. N. Amer., part 4, p. 219, 220.

Pseudolimnophila inornata is not so common as *P. luteipennis* but is found in similar situations. The immature stages are spent in rich organic mud. The only specimens that the writer has reared were taken in

Larch Meadows, near Ithaca, New York, on May 15, 1917, where they were associated with larvae of *Rhamphidia mainensis*, *Pseudolimnophila luteipennis*, *Tipula dejecta*, and other swamp-inhabiting species.

Larva.— Very similar to that of *P. luteipennis*, but body is darker and is conspicuously blotched with whitish, especially on posterior parts of ventral segments. Mouth parts nearly the same in the two species. Antenna (Plate XXXIX, 174) with two very long and slender terminal papillae, one blunt at tip, the other much longer and tapering gradually to tip.

Pupa.— Very similar to that of *P. luteipennis*, but somewhat smaller and darker-colored. Pronotal breathing horns (Plate XL, 177) darker brown, the divergent terminal flaps proportionately a little more elongate, equal to almost one-quarter length of entire horn. Dorsal lobes at base of ovipositor more attenuated.

Nepionotype.— Larch Meadows, Ithaca, New York, May 15, 1917. No. 53–1917.
Neanotype.— Larch Meadows, Ithaca, New York, May 25, 1917. No. 53–1917, cast pupal skin.

Subtribe **Dactylolabaria**

The division Dactylolabaria is proposed for the genus Dactylolabis, a small group of curious crane-flies which are still not well understood. The adult flies bear a striking resemblance to species of the genus Limnophila, but the larvae and the pupae show characters that are not found in the more specialized divisions of the Hexatomini. The type of the genus is *Limnophila montana* O. S. of the eastern United States. Other Nearctic species included are *L. damula* O. S. (western United States), *L. rhicnoptiloides* Alex. (northwestern Canada), *L. cubitalis* O. S. (eastern United States), *L. nitidithorax* Alex. (western United States), and *L. hortensia* Alex. (western Canada).

The immature stages of two European species — *D. wodzickii* (Now.) and *D. denticuláta* Bergr.— have been made known by Nowicki (1867: 340–343) and by Mik (1894), respectively. Their descriptions of the details of the larval head and the lateral spiracles of the abdomen of the pupa are incomplete, however. The larvae of none of the American species have as yet been made known, but the pupae of *D. cubitalis* O. S. were found by Needham and are described hereinafter.

Genus **Dactylolabis** Osten Sacken (Gr. *finger forceps*)

1859 *Dactylolabis* O. S. Proc. Acad. Nat. Sci. Phila., p. 240.

Larva.— Body very depressed, the ventral surface, especially, being greatly flattened. Head capsule compact; mentum not completely divided, its anterior margin with seven teeth. Mandible with but few lateral teeth.

Pupa.— Somewhat similar to pupae of Limnophilaria. Pronotal breathing horns short and cylindrical. In some species, at least, second abdominal segment with a very large and prominent lateral spiracle.

Dactylolabis is a small genus including about thirteen known species which are about equally well distributed in Europe and North America.

Dactylolabis denticulata (Bergr.)

1891 *Limnophila denticulata* Bergr. Mittheil. Naturf. Ges. Bern, p. 132.

The present knowledge of the life history of *Dactylolabis denticulata* is due to the work of Mik (1894), whose paper is cited by other workers, among them Grünberg (1910:54–55).

Larvae and pupae were found on the dark brownish gray chalk cliffs near Steiermark on August 3, 1891. In certain places on the cliffs were broad or narrow bands of black. The larvae and the pupae were found along these dark bands and showed a decided resemblance to their surroundings. The surface of the rock was wet with dripping water, which supported a flora of lowly plant organisms on which the larvae presumably fed. The adherence of the pupa to the last larval skin is of interest since it presumably aids in the emergence of the adult. A similar condition is found in Cylindrotoma.

Larva.— Length, 7 mm.
Width, 2 mm.

Form very depressed (Plate XLI, 183), the ventral surface flattened, almost leechlike. Both dorsal and ventral surface provided with hairs, with longer and more numerous hairs on sides of body. Body covered with small, black, structureless particles of earth or excrement, more numerous near margins of dorsal surface, these particles lacking a definite arrangement and being very firmly attached to the body hairs; when particles are removed, larva is of a greenish gray color, subhyaline. Abdominal segments divided into two rings bearing long hairs which are more conspicuous on sides of body. Head capsule (Plate XLI, 182) small but compact, completely retractile within prothoracic segment. Labrum relatively large and semitransparent, the margins with long hairs; on dorsum on either side a long delicate seta. Mentum chitinized; anterior margin with seven teeth, behind median tooth a brush of hairs. Antenna two-segmented; basal segment cylindrical; second segment button-like, with apex pointed. Mandible three-toothed; a tuft of hairs at prosthecal region. Spiracular disk surrounded by two fleshy welts which are deeply incised medially to appear as four blunt lobes. Spiracles difficult to distinguish in a position of rest, elliptical, margined with blackish brown.

Pupa.— Length, 8 mm.
Width, 1.75 mm.

Coloration blackish; abdomen dark greenish gray.

Pupa (Plate XLI, 181) attached to old larval skin, which in turn remains attached to rock surface. (Just before pupating, the larva sticks itself to the surface by means of its saliva.) Pronotal breathing horns cylindrical, a little swollen at ends. Sheaths of appendages dull and black in color. Leg sheaths attaining end of fourth abdominal segment.

Dactylolabis wodzickii (Now.)

1867 *Rhicnoptila wodzickii* Now. Verh. Zool.-Bot. Ges. Wien, vol. 17, p. 337–354.

The species *Dactylolabis wodzickii* was first found in the high Alpine region of the Hungarian Tatras, at an altitude of from 6000 to 8000 feet, in a region frequented by the wall creeper (Tichodroma). Here the adults and the immature stages were found together on the granite cliffs where water dripped continuously, supporting a considerable algal flora. Associated with the species were other flies, *Liancalus virens* (Scop.) and *Clinocera fontinalis* Hal., as well as *Tricyphona schineri* (Kol.). The degenerate wings of the insects prevent their flying, and they probably live and die close to the place where the eggs are deposited. One fly was observed laying her eggs in the masses of algae in this situation. The larvae live in these masses and pupate in them.

Larva.— Length, 12.5 mm.
Width, 2.4 mm.

Dorsum of body dark greenish brown, with dark longitudinal brown stripes producing a curious pattern of straight and convergent lines; ventral surface almost white, unmarked.

Body depressed, flattened, abdominal segments divided into a narrow basal and a much broader posterior annulus. Head capsule (Plate XLI, 185) compact, massive. Mandible showing but a single inner tooth. Posterior abdominal annuli with two long setae on lateral margins. Spiracular disk (Plate XLI, 186) surrounded by four lobes, the ventral pair longer than the others; these lobes margined with darker chitinized lines and provided with fringes of moderately long hairs. Spiracles not described, and undoubtedly overlooked by the describer.

Pupa.— Length, 12.5–13.5 mm.
Width, 2.6 mm.

Color brown. Pronotal breathing horns short, cylindrical. Wing sheaths ending opposite middle of second abdominal segment. Leg sheaths ending beyond middle of third segment. Abdomen armed with rows of spines (Plate XLI, 184).

Dactylolabis cubitalis (O. S.)

1869 *Limnophila cubitalis* O. S. Mon. Dipt. N. Amer., part 4, p. 229.

Dactylolabis cubitalis is a local species, often occurring in great numbers. In the gorge of Fall Creek near the Cornell University campus this species

can be found in myriads by sweeping the rank herbage in May. The writer has never located the immature stages, but the species was reared by Dr. J. G. Needham at Ithaca, New York, on May 20, 1898. There is no record as to where these larvae occurred, but they are presumably mud-inhabiting forms, or possibly they frequent habitats similar to those described for the two preceding species.

Pupa.— Length of cast skin, about 12 mm.

Pronotal breathing horns (Plate XLI, 187) short, cylindrical, the tips scarcely enlarged. Mesonotum behind with a prominent rounded tubercle on either side of median line, which is set with two spines, a larger outer spine and a small inner spine. Wing sheaths ending opposite apex of second abdominal segment. Leg sheaths ending opposite apex of third abdominal segment, the tarsal sheaths terminating on a common level.

Abdominal segments divided into two rings. Tergites with posterior ring having a transverse row of elongate tubercles, there being about eight on segment 2, about six on intermediate segments (3 to 5), and about four on segments 6 and 7; these tubercles fleshy, but sparsely armed with chitinized spines. Basal ring unarmed. Pleura with a strong tubercle on each ring; a blunt but prominent spiracle at extreme base of posterior ring; this spiracle very prominent on segment 2 (Plate XLI, 188), much exceeding lateral tubercles and being about two-fifths length of pronotal breathing horns. Sternites with about six tubercles on posterior ring. Male cauda (Plate XLI, 189) with tergal lobes slender, running out into acute chitinized points, which are directed caudad, slightly divergent; dorsum of segment 8 with posterior lobes powerful, about equal in size to, or a little larger than, tergal lobes of cauda just described; anterior lobes small, directed caudad and laterad; two large lateral lobes and two smaller ventral lobes. Female cauda with tergal valves moderately elongate, stout, broad at base, narrowed toward tip, where they run out into long, chitinized points directed caudad and slightly dorsad.

Neanotype.— Cast pupal skin, Ithaca, New York, May 20, 1898.
Paratype.— Pupae, cast skins, with type.

Dactylolabis montana (O. S.)

1859 *Limnophila montana* O. S. Proc. Acad. Nat. Sci. Phila., p. 240.

The species *Dactylolabis montana* is common and widely distributed thruout the northern United States. It is a characteristic inhabitant of rocky cliffs, where it rests in crevices on the almost vertical walls. The immature stages have long remained unknown, but during the spring of 1920 W. L. McAtee found a pupal skin and the teneral adult near Washington, D. C. Mr. McAtee writes that the pupa was found in the moss that covers the almost vertical north face of a cliff on Plummers Island; this moss is mostly shaded, and grows on a thin layer of black soil which, at that time of the year at least, is saturated with water. The

pupal skin was not in condition for study, but now that the larval habitat is known it is hoped that more material of the immature stages will become available.

Subtribe **Limnophilaria**

The division Limnophilaria comprises a large and heterogeneous group of species which in their larval and pupal characters grade rather insensibly into the next subtribe, the Hexatomaria, altho the adults of the two subtribes are very distinct.

The larvae of the various species in the group Limnophilae are rather similar to one another. The head capsule is long and narrow, with the lateral plates very slender. The labrum is ample, with several sensory papillae and setae. The antennae (which are two-segmented in the subgenera Phylidorea and Lasiomastix, and probably also in Dicranophragma and others) bear at their tips, in addition to the usual elongate setae, an oval or elongate-oval papilla which is delicately sculptured. The mental region is feebly chitinized, and consists of two short longitudinal bars articulated at their cephalic ends with a transverse bar which functions as the mental plate; this bar, or plate, is usually delicately grooved with parallel striae, a type of articulation that allows for great distention of the gular region in feeding. The mandibles are powerful chitinized hooks bearing two or more acute or flattened teeth at about midlength. The outer lobes of the maxillae project far cephalad as pale flattened blades.

The spiracular disk, in the primitive condition, is squarely truncated and is surrounded by five subequal lobes which are fringed with rather short hairs. The dorso-median lobe is lost in most species, but the two pairs of lobes are more or less preserved in the other species known to the writer, altho the lateral pair is sometimes reduced to a mere fringe or tuft of hairs. The terminal fringes of the ventral lobes are often greatly elongated, and fanlike. The anal gills are four in number, retractile, and rarely conspicuous. As is usual in many mud- or sand-inhabiting species of Tipulidae, the larvae are capable of greatly distending the subterminal abdominal segment. This segment is often provided with numerous transverse rows of fine points, and its inflation assists in the larva's progression thru the soil.

The larvae of the group are carnivorous, and almost without exception are exceedingly agile and snakelike in their motions.

The pupae of the group Limnophilae have the pronotal breathing horns usually small, or at least not greatly elongated. The abdomen is often greatly depressed, with the lateral margins flattened and carinate and the segments incised. In the species of the subgenus Phylidorea the segments of the abdomen are armed with rows of long, slender spines.

The group Ulomorphae seems to be closely related to the other members of the division, but the immature stages present some curious conditions which it is difficult to correlate with the same structures in the group Limnophilae. The writer has removed a group of species from the old genus Limnophila, and has placed these in the genus Pilaria Sintenis.

In the larvae of the group Ulomorphae, the epipharynx and the maxillae are densely hairy. The maxillary lobes are slender. The mandibles are hinged at about midlength, the basal segment being concave on its inner face to receive the mandibular blade when in a position of rest. The mandibular blade has one, or sometimes two, elongate acute teeth at the base. The mental region is not chitinized. The spiracular disk is surrounded by four lobes, of which the lateral pair are often very reduced; the inner faces of the lateral lobes are capable of close approximation, so that when they are closely applied the spiracles are contiguous. The pupae have the pronotal breathing horns very elongate, with their tips split into two flattened divergent lobes, as in Pseudolimnophila and a few tipuline forms.

The following keys separate the genera and the subgenera of the subtribe Limnophilaria:

Larvae

1. Mental region not chitinized; maxillae and epipharynx fringed with conspicuous, long, golden-yellow hairs; mandibles hinged; head capsule with dorsal plate spatulate at its tip. (Group *Ulomorphae*, p. 869)..2

   Mental region a narrow, transverse, chitinized bar, finely striate; maxillae and epipharynx without conspicuous hairs; mandibles not hinged; head capsule not as described above. (Group *Limnophilae*, p. 858)..................................3

2. Length under 12 mm.; basal tooth of mandibular blade nearly half the length of blade. *Ulomorpha* O. S. (p. 869)

   Length over 14 mm.; basal tooth of mandibular blade about one-third or less the length of blade...*Pilaria* Sint. (p. 872)

3. Spiracular disk almost squarely truncated, surrounded by five subequal lobes producing an eriopterine appearance..........................*Dicranophragma* O. S. (p. 861)

   Spiracular disk obliquely truncated, surrounded by two pairs of lobes of which the lateral pair are the shorter...4

4. Mandibles with two or three acute teeth at about midlength; epipharynx with a circular area bearing two biarticulate papillae......................*Phylidorea* Bigot (p. 866)

   Mandibles with three or four flattened and truncated teeth along blade; epipharynx without papillae as above...............................*Lasiomastix* O. S. (p. 863)

Pupae

1. Pronotal breathing horns very long, cylindrical, the tips split into divergent flaps. (Group *Ulomorphae*, p. 869)........2
   Pronotal breathing horns not elongate-cylindrical. (Group *Limnophilae*, p. 858)........3
2. Abdominal segments with tubercles or spines only near posterior margins of segments. *Ulomorpha* O. S. (p. 869)
   Abdominal segments with three or four pairs of blunt, naked tubercles. *Pilaria* Sint. (p. 872)
3. Abdominal segments depressed, lateral margins flattened, carinate, segments deeply incised........4
   Abdominal segments not depressed nor incised; pronotal breathing horns bicolored. *Dicranophragma* O. S. (p. 861)
4. Abdominal segments with rows of acute slender spines; pronotal breathing horns very short, semicircular in outline, bluntly rounded at their tips.. *Phylidorea* Bigot (p. 866)
   Abdominal segments without such slender spines; pronotal breathing horns short, broad, slightly compressed, tips a little pointed........*Lasiomastix* O. S. (p. 863)

Group **Limnophilae**

Genus **Limnophila** Macquart (Gr. *swamp* + *friend*)

1834 *Limnophila* Macq. Suit. à Buff., vol. 1, Hist. Nat. Ins., Dipt., p. 95.
1854 *Phylidorea* Bigot. Ann. Soc. Ent. France, p. 456.
1861 *Limnomya* Rond. Dipt. Ital. Prodr., vol. 4, p. 11.

Larva.— Form slender. Spiracular disk surrounded by five, or more commonly four, lobes, the ventral pair the longer and fringed with long, delicate hairs. Anal gills four, not conspicuous. Head capsule flattened, very dissected, with plates narrow. Mandible not hinged, curved, chitinized, on cutting edge with a few acute or flattened teeth. Maxilla with outer lobe produced into a flattened projecting blade. Antenna two-segmented, at its tip with a short or elongate-oval papilla which is delicately sculptured. Mentum a transverse chitinized crossbar which is finely grooved.

Pupa.— Cephalic crest setiferous. Pronotal breathing horns usually small, flattened, tips not split. Mesonotum convex or flattened above. Abdominal segments in some cases armed with tubercles or spines.

The genus Limnophila comprises a very extensive group of crane-flies (more than one hundred and fifty species), which are found in most parts of the world but are apparently more numerous in the temperate regions. The adult flies seem to be closely related, but the immature stages are so varied in structure as to make it appear that the group must be a heterogeneous one and the similarity of the adults a result of convergent evolution.

The adult flies may be found resting on rank vegetation. Several of the species (*Limnophila ultima,* for example) swarm in small groups of from fifty to sixty individuals, copulation taking place in the air, as is discussed more fully on page 711.

The immature stages of several species have been made known, but there are still very considerable gaps in the present knowledge. The larvae are among the most carnivorous of all crane-fly larvae. The feeble chitinization of the mental region allows for great distention, and oftentimes the prey of these larvae consists of forms that are nearly as large as the captors themselves.

The data regarding extra-American species may be summarized as follows:

Limnophila bryobia Mik (1881:205–206) was reared from moss, taken in the Auckland Islands, near New Zealand, in the summer (December to February) of 1874–75. The moss was dried and then placed in a temperature of from 12° to 15° Réaumur. In March of 1879 an adult fly appeared. This long interval of more than four years was supposed by Mik to have been passed by the insect as a larva, the dry moss furnishing the food. Possibly the eggs were carried over for a long period before hatching.

Limnophila sinistra Hutton, of New Zealand, has been discussed in some detail by Hudson (1920:33–34), who states that this species is common in most dense forests thruout the country. The larva inhabits fallen tree-trunks in an advanced state of decay, forming burrows between the soft, decayed part and the harder part of the wood. It is about 25 millimeters in length, cylindrical, tapering toward the head, which is very small, and furnished with two minute jaws and a pair of very short antennae. There are eleven visible body segments. The extremity of the last segment is truncate and deeply excavated, the concavity being protected by five converging spines, which can be spread out or drawn inward at the will of the insect. Pedal warts occur on the undersides of all the segments except the three immediately following the head and the terminal segment. The pupa is about 12 millimeters in length, and rather stout. The breathing horns are about one-third the length of the wing sheaths, and are moderately stout and strongly recurved. There are two dorsal rows of hooks on each exposed abdominal segment and one ventral row near the terminal extremity. The valves of the ovipositor are strongly recurved and very stout. The head and the thorax are dark brownish black, highly polished; the abdomen is grayish ocherous, darker in the middle; the ovipositor and the terminal segments of the posterior tarsi are reddish. The pupa rests in a burrow made by the larva near the surface of the log.

Edwards has decided that this insect and a few related species should be placed in a new genus. The affinities of the fly, to judge from the details supplied by Hudson, are with the Epiphragmaria rather than with the Limnophilaria, but until more details are forthcoming it cannot be definitely referred to that division.

Limnophila (*Phylidorea*) *ferruginea* (Meig.), of Europe, is closely allied to *L. adusta* (page 867), and is of especial interest as being the type of the subgenus Phylidorea. It was reared by De Meijere (1916:204–206) from larvae found living between saturated decaying leaves along the banks of watercourses. Further mention of the species is made under the discussion of the subgenus Phylidorea (page 866).

Limnophila hyalipennis (Zett.), of Europe, was found by Beling (1886:198–199) in piny woods, where the larvae live in old ant hills or in piles of earth thrown up by wagon wheels. The apparent lack of pupal breathing horns in this species is discussed on page 755. The European species *L. lineola* (Meig.) (Beling, 1879:54 and 1886:199–200), *L. nemoralis* (Meig.) (Beling, 1886:200–201), and *L. ochracea* (Meig.) (Beling, 1886:202) are all found in damp earth along the margins of woodland streams or in damp spots in the woods. Larvae of *L. dispar* (Meig.) were found by Perris (1849:331) living in the hard, withered stalks of an umbellifer, *Angelica sylvestris* Linn., where they hollowed out long passages in the pith. (This reference is cited by Mik, 1881:204, and by Osten Sacken, 1869:201–202.) *Limnophila pallida* Bel. was reared by Beling (1873a:557) from larvae living in a decaying ash trunk.

The reference to *Limnophila platyptera* Macq. given by Heeger (1854) is considered by Osten Sacken (1869:4, 202) to refer to a mycetophilid, probably Bolitophila.

The American species that are now known are considered in the following pages. In addition, *Limnophila unica* O. S. has been bred from larvae found in decaying wood.

It is very probable that some of the species listed above, as well as many of the limnophiline forms that are still unknown as regards their immature stages, will be found to belong to some one or other of the remaining divisions of the tribe, rather than to the Limnophilaria as here restricted. This group requires more careful study than does any other division of crane-flies.

(Subgenus **Dicranophragma** Osten Sacken)

1859 *Dicranophragma* O. S. Proc. Acad. Nat. Sci. Phila., p. 240.

Larva.— Form short and stout. Spiracular disk surrounded by five short lobes, the ventral pair the longest, the dorsal lobe very blunt; disk surrounded by a fringe of delicate hairs which are longest at tips of lobes. Head capsule of the hexatomine type. Mandible powerful, prolonged into a strong hook with a large acute tooth just beyond midlength. Maxilla very long and slender. Mentum chitinized, consisting of a narrow transverse bar which is ribbed with fine parallel grooves.

Pupa.— Cephalic crest prominent, each half with three setae. Pronotal breathing horns short, cylindrical, or slightly narrowed to a blunt tip. Mesonotum convex, unarmed. Wing sheaths short, broad, ending before tip of second abdominal segment. Leg sheaths moderate in length, ending just beyond base of fourth abdominal segment, hind tarsi a little longer than the others. Abdominal segments divided into two rings; posterior ring with a subterminal transverse armature, on dorsum consisting of numerous setiferous tubercles, on pleura consisting of two or three groups of setiferous tubercles; basal ring with about eight slender tubercles on dorsal surface. Spiracles present, but evidently nonfunctional. Dorsum of segment 8 with four slender tubercles.

Dicranophragma is a well-defined group of the genus Limnophila, with about six known species whose center of distribution seems to be in the Oriental region. The type of the subgenus, *Limnophila* (*Dicranophragma*) *fuscovaria*, discussed in detail below, is the only described New World form. The immature stages are spent in rich organic mud in cool, shaded woods.

Limnophila (*Dicranophragma*) *fuscovaria* O. S.

1859 *Limnophila (Dicranophragma) fuscovaria* O. S. Proc. Acad. Nat. Sci. Phila., p. 240.

The adult flies of *Limnophila fuscovaria* may be easily distinguished by their broad, heavily spotted wings and the strong supernumerary crossvein in cell R_2. They may be swept from rank vegetation in cool, shaded woods. The larva has the body stouter and less elongate than is usual in this group of species, but it possesses the same snakelike movements as its near relatives. The pupal duration is not longer than eight days (June 8 to 16, in 1917).

Larva.— Length, 6.8–7.2 mm.
Diameter, 0.7–0.8 mm

Coloration light golden-yellow; maxillary lobes yellow; spiracular disk lined with dark brown. Body rather short and stout, not of the exceedingly elongate type of the Eriopterini, gradually narrowed to anterior end (Plate XLII, 190); prothoracic segment truncated anteriorly;

when head is retracted, tips of maxillae projecting from prothoracic orifice. Seventh abdominal segment with a transverse fringe of stiff hairs on the sides, these directed laterad and slightly caudad. Body noticeably constricted just before last segment. Spiracular disk (Plate XLII, 195) surrounded by five lobes, and in superficial appearance decidedly eriopterine rather than hexatomine; ventral lobes the longest but still much shorter than is usual in this tribe, slightly divergent, inner face with a double, V-shaped, dark brown mark, inner arm of V narrow, outer arm more expanded, especially at proximal ends, one large inner and two smaller outer sensory bristles at apex of V; lateral lobes narrow, with a V-shaped mark similar to that of ventral lobes but narrower and darker; dorsal lobe broad, the inner face indistinctly lined with parallel, dusky, longitudinal stripes; all five lobes surrounded by a fringe of long, delicate hairs lying just outside brown marks, these hairs longest at tips of lobes and continuous around disk. Spiracles circular, rather widely separated; ring broad, light yellow, narrowly margined outwardly with black. Anal gills four, short and stout.

Head capsule (Plate XLII, 191) very dissected, consisting of six elongate slender plates, three on either side, articulating at a point laterad of mental plate. Labrum (Plate XLII, 192) large; anterior margin indistinctly trilobed, the median lobe hairy; on the ventral, or epipharyngeal, surface, on either side, a slender cylindrical papilla, subhyaline, directed cephalad; sides of epipharynx with a tuft of long setae. Mentum chitinized, consisting of two lateral rods and an anterior transverse bar which is finely ribbed with parallel lines. Immediately dorsad of mentum two roughened papillae (prementum) directed cephalad; esophagus retrorsely roughened. Antenna (Plate XLII, 193) stout, in caustic-potash preparations almost hyaline, tipped with an elongate cylindrical lobe distad of which is a small setiferous tubercle with two long, delicate setae exceeding antennae in length. Mandible (Plate XLII, 194) powerful, very deep at base, produced into an acute, strongly curved tip; just beyond midlength a very large, acute tooth which is about one-third length of apical point, in its angle a small, hyaline, flattened, leaflike blade with a truncated apex; basad of large tooth two or three gradually smaller teeth. Maxilla with outer lobes stout, broad at base, gradually narrowed to tip, which is cut off by a constriction into a semi-oval structure; palpi on inner dorsal face of maxillary lobe at about midlength, short, semi-globular, with abundant sensory papillae; when head is completely retracted, the long, pale, slightly divergent tips of maxillary lobes projecting from orifice.

Pupa.— Length of cast skin, about 6 mm.

General coloration dark brown; pronotal breathing horns almost black, with apical fourth conspicuously light yellow; abdominal incisures pale.

Cephalic crest large and prominent, with three long setae on outer face. Labrum blunt at apex. Labial lobes with a blunt point on either side, these directed proximad and caudad. Maxillary palpi broad at base, suddenly narrowed to the long, cylindrical tip, which is darkened. Antennae rather short. Pronotal breathing horns (Plate XLIII, 196) stout, short, almost straight, broad basally, tapering gradually to the blunt tips. Wing sheaths very short and broad, ending before tip of second abdominal segment. Leg sheaths short, extending to just beyond base of fourth abdominal segment; all the tarsi ending about on a level, or outer sheaths a little the longer.

Abdominal segments (Plate XLIII, 198) each divided into two rings by a false constriction, basal ring about two-thirds length of posterior ring. Basal ring on dorsum with a transverse row of about eight slender, blunt tubercles before caudal margin; on pleura a similar but larger tubercle opposite basal ring, this tipped with a long, delicate seta. Sternum unarmed. Posterior ring on dorsum with a subterminal row of blunt tubercles, simple or bifid, often approximated or crowded, bearing one or two long setae; near base of tergum, opposite spiracle, a setiferous tubercle; on pleura, opposite base of posterior ring and nearer dorsum than sternum, a vestigial spiracle with a double setiferous tubercle ventrad of it; near caudal margin of pleura two or three compound multisetose tubercles (Plate XLIII, 197) or aggregations of simple tubercles, which are largest on seventh segment. On sternum, two slender tubercles on either side, near base of posterior ring. Female cauda (Plate XLIII, 201) elongate, with the tergal valves a little longer than the sternal valves; each of tergal valves with a small tubercle at base. Male cauda (Plate XLIII, 199 and 200) with the ventral lobes blunt, the dorsal lobes a little longer and ending in an acute point; a tiny tubercle on either side at base of dorsal lobes. Dorsum of segment 8 with a trapezoid of four conspicuous lobes ending in truncated tubercles; anterior pair of lobes smaller and a little more widely separated than posterior pair.

Nepionotype.— Ithaca, New York.
Neanotype.— Ithaca, New York, May 31, 1917. No. 57-1917.
Paratypes.— Pupal skins, June 11, 1917 (No. 99-1917), June 16, 1917 (No. 132-1917). Abundant larvae, with nepionotype.

(Subgenus **Lasiomastix** Osten Sacken)

1859 *Lasiomastix* O. S. Proc. Acad. Nat. Sci. Phila., p. 233.

Larva.— Body slender, with pencils of stiff setae on lateral margins of thorax. Spiracular disk with four lobes, the ventral pair a little the longer and bearing a fringe of long, delicate hairs, these about twice length of lobes. Anal gills short and stout. Head capsule of hexatomine type. Mandible powerful, cutting edge with a single row of three or four flattened, bladelike teeth. Maxilla very long and slender. Antenna elongate, at tip with a small elongate-oval papilla whose surface is delicately sculptured. Mentum chitinized, a strong transverse bar which is ribbed with fine parallel grooves.

Pupa.— Cephalic crest very small, inconspicuous, bilobed. Pronotal breathing horns short, broad, somewhat compressed, a little pointed at apex. Mesonotum unarmed. Abdominal segments depressed, armed with numerous tubercles or small spines, these being most abundant on posterior annuli of segments.

The subgenus Lasiomastix includes but six known species, three of which are from eastern North America. *Limnophila* (*Lasiomastix*) *macrocera* is common and widely distributed thruout the Eastern States. *L.* (*L.*) *tenuicornis* O. S. and *L.* (*L.*) *subtenuicornis* (Alex.) are found only in the Northeastern States and are more local in their distribution. The immature stages of *L.* (*L.*) *macrocera* are spent in rich organic mud. They are very similar to those of the subgenus Phylidorea.

Limnophila (Lasiomastix) macrocera (Say)

1823 *Limnobia macrocera* Say. Journ. Acad. Nat. Sci Phila., vol. 3, p. 20.

Limnophila macrocera is a common swamp-inhabiting crane-fly, the larvae living in organic mud. At Orono, Maine, the writer found larvae of this species associated with larvae of *Bittacomorpha clavipes, Pilaria tenuipes, P. recondita, Erioptera chlorophylla,* and other crane-flies, as well as with leeches, snails, worms of many kinds, and other forms of life. The larva is similar to that of other related species. When placed in water it is very active and has the habit of darting the anterior quarter of its body from one side to the other, suggesting the striking of a reptile. The pupal duration is not more than eight days (June 24 to July 2, June 28 to July 6).

Larva.— Length, 14.5–15 mm.
Diameter, 1.4 mm.

Coloration, pale yellowish white.

Body terete, narrowed toward both ends but more noticeably toward anterior end. Integument covered with a dense appressed pubescence. Chaetotaxy as follows: two stout setae on both dorsal and ventral margins of prothoracic orifice; thorax with pencils of stiff setae near anterior margins of segments, two large lateral tufts and a smaller ventral pair; abdominal segments with a pencil of similar bristles on ventro-lateral margins, one on anterior half, the other midlength, of each ring; a seta at posterior lateral angles of sternites; four setae in a transverse row near posterior margin of tergites, the lateral pair the larger; lateral margins of cauda near base of lateral lobes and above gills with pencils of blackish setae; basal part of segments on both sternum and tergum with transverse parallel rows of fine scabrous points, this area very narrow on second abdominal segment, consisting only of three or four rows, the areas gradually becoming broader and the rows more numerous, there being on sixth and seventh segments about 28 to 30 rows which occupy nearly the basal third of segments.

Spiracular disk (Plate XLIV, 208) surrounded by four lobes; ventral pair the longest, lateral pair a little shorter; ventral lobes near tips with a brush of delicate, exceedingly long hairs which curl into loops at tips, the longest of these hairs about twice length of lobes bearing them; this fringe of hairs continuous around disk, longest at ends of lobes, gradually shortened toward their bases but not interrupted; lateral lobes with terminal hairs a little shorter but still longer than lobes themselves; inner faces of lobes delicately margined with dark brown, those of ventral lobes having the outer lateral margins the broadest. Spiracles rather small, located at base of lateral lobes. Anal gills four, very stout and plump.

Head capsule with a framework of long, slender plates, as is usual in this group. Labrum (Plate XLIV, 205) broadly transverse; anterior margin irregularly rounded; anterior median area truncated, with the lateral angles slightly projecting, cut off squarely, each with a small, hyaline, sensory papilla; laterad and caudad of each, two sensory papillae, the innermost elongate-cylindrical, more than twice length of short, oval, outer one. Epipharyngeal

region roughened by tiny groups of parallel ridges. Mental region consisting of a heavily chitinized transverse bar which is delicately grooved, enlarged at ends, and articulating with a small ventral bar. Antenna (Plate XLIV, 206) long and slender; basal segment short and broad; second segment elongate-cylindrical, bearing at its tip a small, hyaline, sensory papilla which appears delicately crosshatched by fine impressed lines, this papilla elongate-oval with the apex broadly rounded; a long hair near base of this papilla and about twice its length. Mandible (Plate XLIV, 207) long and powerful, the tip produced into a slender point, the cutting edge at about midlength with a single row of three or four flattened, bladelike teeth which are truncated at their tips, these teeth varying considerably in their shape and relative proportions. Maxilla with outer lobe elongate, the base strongly chitinized, this chitinized part continuing up margin of lobe almost to tip, the apical part nearly hyaline; at about midlength, the small palpus and a long seta. Esophagus enlarged, the walls thickened and roughened.

(A slide of a larva that was supposed to belong to this species differs considerably from the material described above. The antenna is much shorter, with the apical tubercle much larger and elongate-cylindrical; the mandible has the teeth fewer and more acute, quite as shown by De Meijere for *Limnophila* [*Phylidorea*] *ferruginea*. It is probable that this species likewise is a Phylidorea.)

Pupa.— Length, 14–16 mm.
Width, d.-s., 1.8–2 mm.
Depth, d.-v., 1.9–2.2 mm.

Breathing horns pale whitish brown, a little darker at base; remainder of body dark brownish black, abdomen a little lighter-colored; incisures of segments, and pleural line, pale.

Cephalic crest very small, inconspicuous, bilobed, each principal lobe subdivided into two smaller lobes terminating in a small seta; another seta on anterior face. Labrum rather blunt and truncated at apex. Labial lobes terminating in sharp points projecting proximad. Maxillary palpi short and stout, tapering to blunt tips (Plate XLV, 210). Antenna of male elongate, reaching to beyond midlength of wing sheath; antenna of female short, ending at about one-fourth length of wing sheath. Segments of antenna cylindrical, unarmed.

Pronotal breathing horns (Plate XLV, 209) short, broad, somewhat compressed, a little pointed at tip. Thorax broad and deep, the pronotum flattened, carinate medially. Mesonotum high, convex, transversely wrinkled. Wing sheaths ending some distance before tip of second abdominal segment. Leg sheaths short, ending before tip of third abdominal segment, the hind legs a little longer than the other legs, which end about on a common level.

Abdomen depressed, lateral margin carinate. Abdominal segments distinct, incised, each segment divided into two annuli, basal one about half length of posterior one. Basal ring on dorsum with a transverse single, or somewhat double, row of small subacute spines, which are more numerous and larger on mid-dorsal area. Pleura unarmed. Sternum with an oblique flattened lobe or wing on each side, directed caudad and proximad; between these lobes a more or less broken transverse row of from six to twelve slender tubercles. Posterior ring on dorsum with numerous small scattered tubercles. Pleura with a small circular spiracle near base and close to dorsal margin; a slender seta near spiracle and ventrad of it;

two other setae caudad of spiracle; at caudal margin a solitary seta close to ventral margin. Sternum with scattered slender tubercles, on segment 3 these appearing as a longitudinal row of about ten alongside the hind legs; between this lateral longitudinal row and the scattered discal tubercles, a bare space, at anterior end of which is a large, stout, setiferous tubercle; a subterminal transverse row of about fifteen acute black spines; on terminal segments the lateral longitudinal rows interrupted, or, on the seventh segment, lacking, on seventh segment the subterminal armature of both dorsum and sternum more powerful, especially the intermediate spines of sternum, which are very large; numerous setae scattered along rows. Segments 3 to 8 on ventral surface of posterior ring with a circular disklike area, median in position and at about two-thirds length of ring. (In some specimens, especially females, the discal tubercles on the posterior ring are much smaller and lie in longitudinal rows.) Male cauda (Plate XLV, 211) with tergal valves slender, elongate, slightly divergent, tapering to the acute tips, which bear a small subterminal seta; sternal valves short, blunt, with a flattened oval lobe between valves of sternum; eighth segment on dorsum with a trapezoid of four very long, slender, pointed lobes, which are provided with delicate hairs, the posterior pair of lobes longer, stouter, and lying closer together; just above anterior pair of lobes a blunt setiferous tubercle; pleural region of segment 8 with two spines; a small seta cephalad of these spines; sternal region of segment 8 with two widely separated setiferous tubercles. Female cauda (Plate XLV, 212) with tergal valves elongate, narrowed at tips, and armed with sharp, black spines; a few small setae before tips; sternal valves short, blunt, narrowed at tips.

Nepionotype.— Orono, Maine, July 19, 1913.
Neanotype.— With type larva, July 17, 1913.
Paratypes.— Larvae, with type larva, June 13 to July 27, 1913. Pupae, June 9 to July 22, 1913.

(Subgenus **Phylidorea** Bigot)

1854 *Phylidorea* Bigot. Ann. Soc. Ent. France, p. 456.

The immature stages of the type species of Phylidorea, *Limnophila* (*Phylidorea*) *ferruginea* (Meig.), were described by De Meijere (1916: 204–206). In Holland, larvae were found in April on the banks of a ditch, where they were living between decaying leaves. The larvae are cylindrical, and are from brownish yellow to brown in color. The antennae are described as three-segmented, the apical papilla being considered as a segment. The labrum bears on the epipharyngeal surface a median projection provided with two conspicuous biarticulate lobes. The outer lobes of the maxillae project as flattened blades. The mandibles are powerful and strongly curved, and have a group of small lateral teeth at about midlength.

The pupa is about 10 millimeters long and is blackish brown in color. The pronotal breathing horns are almost semicircular and are yellowish

brown in color. The abdomen is depressed, with sharp lateral margins. The abdominal armature is described as consisting of small hairs instead of slender spines as in the American species of this subgenus.

In the Nearctic fauna, the subgenus Phylidorea includes *Limnophila adusta, L. similis* Alex., *L. novae-angliae* Alex., *L. lutea* Doane, *L. terrae-novae* Alex., *L. costata* Coq., *L. fulvocostalis* Coq., *L. insularis* Johns., and probably other western species. It seems quite possible, moreover, that the species allied to *Limnophila lenta* O. S. also belong here.

Limnophila (*Phylidorea*) *adusta* O. S. (supposition)

1859 *Limnophila adusta* O. S. Proc. Acad. Nat. Sci. Phila., p. 235.

A larva of a crane-fly that is almost certainly a member of this genus was taken at Ithaca, New York, on May 30, 1917, in company with a Ulomorpha (No. 88–1917). An unknown pupa was taken in the sedge association on the Bool hillside, Ithaca, on June 4, 1917. It was not reared and its identity can only be surmised, but there can be little doubt of its relationship with Phylidorea.

Larva.— Length, 8.6–9 mm.
Diameter, 0.8 mm.

Coloration a deep saturated orange-yellow, the body with silky iridescent reflections.

Body a little narrowed at both ends. Integument with a long, appressed, golden pubescence. Numerous long setae and pencils of hairs on body, usually at about midlength of, or on posterior half of, the segments; posterior margin of each segment elevated into a prominent transverse ridge of hairs. Spiracular disk surrounded by four lobes, ventral pair about twice length of lateral pair; ventral lobes with a rather narrow, dark brown line on inner face; outer margin fringed with very long dark hairs which are somewhat paler at their bases, this fringe of hairs longest at tips of lobes, where it reaches a length of about eight or ten times length of lobe; hairs shorter toward base of lobe; a stiff sensory bristle on outer face of lobe, rather far back from tip; lateral lobes similar, with the fringe of hairs yellow and about twice length of lobes. Spiracles of medium size, directed toward each other. Anal gills four, fleshy, pale in color, posterior pair longer than anterior pair.

Head capsule of hexatomine type, the dorsal plates narrowly interrupted on mid-dorsal line behind clypeal-labral sclerite. Labrum very large, anterior margin provided with eight or ten papillae and setae. Epipharyngeal region having a large, median, circular area which is slightly elevated and bears two bisegmented cylindrical papillae. Mental region as usual in the genus, consisting of three hinged bars forming three sides of a rectangle, the anterior transverse bar delicately grooved. Antenna two-segmented, second segment narrower than first and bearing at its tip an elongate sculptured papilla and a long seta. Mandible of hexatomine type, a powerful curved hook, at about midlength of which is an

acute tooth; in axil of latter a small flattened blade which is slightly widened outwardly and has the tip truncated. Maxillary lobe broad at base, tapering to narrow tip.

Pupa.— Length, 12 mm.
Depth, d.-v., 1.6 mm.

Similar to *Limnophila macrocera* in general shape and color, differing as follows:

Labrum broadly obtuse at tip. Pronotal breathing horns (Plate XLIII, 203) very short, stout but flattened, constricted beyond midlength, and with a row of breathing pores around apex; pronotum and mesonotum carinate medially in front; wing pad showing venation rather clearly, cell M_1 deep, basal deflection of Cu_1 beyond midlength of cell *1st* M_2. Abdominal segments with lateral margins very deeply incised, the carinate lateral margins very accentuated, appearing as thin, flattened wings (Plate XLIII, 204). Armature of abdomen consisting of abundant elongate, acicular spines, some of which are sinuously twisted; on basal ring these spines appearing as a subterminal transverse row on both dorsum and sternum; on posterior ring, besides the subterminal transverse row, spines are scattered over surface in more or less distinct longitudinal rows; at lateral carina a group of about a dozen long spines at caudal margin, as well as a powerful spine below level of spiracle on extreme margin of carina; ventrad and caudad of this, three long setae, two close beneath spine and the third underneath spiracle. Female cauda (Plate XLIII, 202) about as in *Limnophila macrocera*, but sternal valves divergent at their tips; eighth segment with a trapezoid of dorsal lobes about as in *L. macrocera*, but sternum with four stout spines bearing setae on their sides; a blunt median lobe near base of eighth sternite.

(Described from a female pupa taken on Bool's hillside, Ithaca, New York, on June 4, 1917, where it was associated with a characteristic swamp-inhabiting crane-fly fauna — *Bittacomorpha clavipes*, *Pseudolimnophila luteipennis*, *Limnophila macrocera*, *Pilaria recondita*, and *Prionocera fuscipennis*.)

(Subgenus **Limnophila** Macquart)

1834 *Limnophila* Macq. Suit. à Buff., vol. 1, Hist. Nat. Ins., Dipt., p. 95.
1863 *Poecilostola* Schin. Dipt. Austriaca, vol. 2, p. 551.

Limnophila is the typical subgenus of the group, the type having been designated as *Limnophila pictipennis* by Westwood in 1840. No species of this subgenus have yet been described from North America.

The larva of *L. punctata* (Meig.) was described by Beling (1886:195–197) and by Gerbig (1913:158–161) as living in wet earth, by Scheffer (1848:10) and by Cameron (1917:63) as living in decaying wood. Gerbig found larvae in sandy soil near both standing and flowing water. The larvae are very active, are rust-brown in color, and attain a length of 15 millimeters with a diameter of from 1.5 to 2 millimeters. The body is provided with several setae and setiferous projections. The spiracular disk (Plate XLVI, 214) is surrounded by four subequal lobes and an additional reduced dorso-median lobe; all of these lobes are fringed with long

hairs, and each of the four paired lobes has a sensory bristle near the tip. The four anal gills are not very prominent.

The head capsule is of the hexatomine type. The mandibles are sickle-shaped, with two small, broad, blunt, sawlike teeth just beyond midlength.

Brauer (1883:55) found the larvae of another species — *L. pictipennis* (Meig.), the type of the genus — between wet decaying leaves in bogs. His figure of the head capsule (1883, pl. 1, fig. 10) shows a typical hexatomine head (Plate XLVI, 213). Beling (1879:51–52) found this species in the sand of a small, dried-out brook bed.

Group **Ulomorphae**

Genus **Ulomorpha** Osten Sacken (Gr. *Ula* + *shape*)

1869 *Ulomorpha* O. S. Mon. Dipt. N. Amer., part 4, p. 232.

Larva.— Form slender. Body covered with a rich golden-yellow pubescence. Spiracular disk surrounded by four unequal lobes, the ventral pair the longest, lying subparallel, fringed with exceedingly elongate hairs. Spiracles small. Head capsule narrow, the dorsal plate narrow, at tip expanded into a spatula. Mandible hinged, blade very long and slender, with a single very long lateral tooth at its base. Maxilla densely golden hairy, outer lobe projecting, bladelike. Antenna with a very long, tapering, apical papilla. Mentum not chitinized.

Pupa.— Cephalic crest prominent, each lobe with three setae. Pronotal breathing horns very long and slender, sinuous, cylindrical, at apex split into two flattened divergent lobes. Mesonotum short, very convex, unarmed. Wing sheaths attaining end of second abdominal segment. Leg sheaths short, ending before tip of third abdominal segment; hind tarsi a little longer than the others. Abdominal segments divided into two rings, posterior ring with a subterminal transverse armature of stout black spines and a few long setae; sternal armature stronger than that of dorsum. Pleura armed with a few similar spines. Acidothecae of ovipositor very long and slender. Dorsum of segment 8 with a trapezoid of four lobes.

The genus Ulomorpha includes five known species, the genotype, *Ulomorpha pilosella*, of the eastern United States, and four western North American species. The immature stages of the genotype are spent in rich organic mud in shaded situations.

Ulomorpha pilosella (O. S.)

1859 *Limnophila pilosella* O. S. Proc. Acad. Nat. Sci. Phila., p. 242.

Ulomorpha pilosella is not uncommon in cool Canadian woods thruout northeastern North America, and the adult flies may be swept from

rank vegetation in such haunts. The flies bear a marked resemblance to the species of the subgenus Lasiomastix of the genus Limnophila, but the pupae, especially in the structure of the pronotal breathing horns, are quite distinct. The larvae are different from the related and somewhat similar larvae of the subgenus Dicranophragma of the genus Limnophila, of Penthoptera, and of similar hexatomine genera, in their pale whitish yellow coloration instead of the deep saturated yellows and oranges of the genera mentioned. All, however, have the quick, restless movements so characteristic of this group of crane-flies. Larvae found on Bool's hillside, Ithaca, New York, on May 14 and 23, 1917, transformed to adults on June 9.

Larva.— Length, 8.5–9 mm.
Diameter, 0.5–0.6 mm.

Coloration pale whitish yellow, the eighth abdominal segment suddenly whitish.

Form slender. Body covered with a dense golden-yellow pubescence. A transverse fringe of stiff, erect, short hairs at posterior margin of prothorax. A number of pencils of setae or solitary bristles on sides of segments, one on each annulus, longest near posterior margins of segments. Behind these setae, tufts of small hairs. Spiracular disk (Plate XLVI, 219) surrounded by four lobes; ventral pair the longest, lying subparallel to each other, outer margin fringed with long, delicate hairs, those near tip coarse and easily broken, some of the hairs at tips exceedingly elongate; inner face of ventral lobes heavily suffused with dark brown, this color more intense proximally; lateral lobes short, with an apical fringe of coarse yellowish setae. Spiracles very small, widely separated, located at base of lateral lobes. Anal gills four, very slender, pale in color, the posterior pair a little the longer. On sternum of eighth abdominal segment, before gills, a transverse row of four long, coarse setae.

Head capsule (Plate XLVI, 215) very long and narrow, the dorsal plate slender, at end expanded into a spatula; lateral plates a little shorter than dorsal plate. Labrum (Plate XLVI, 216) and epipharynx broadly transverse, projecting, the anterior margin narrower, truncated, on either side near base with a brush of long hairs; disk of epipharyngeal region with four setae, posterior pair a little the closer together; a few tiny papillae on ventral surface; clypeal region emarginate, with two large setae near anterior margin and another immediately behind base of antenna. Mental region not readily distinguishable in the material available, but at the most with little or no chitinization. Antenna (Plate XLVI, 217) with basal segment cylindrical, a little narrowed medially, the truncated apex with about two or three long setae and a very long, hyaline, sensory papilla which tapers gradually to apex, this papilla about three times length of segment bearing it. Mandible (Plate XLVI, 218) hinged, the base slender but powerful, with the inner face deeply concave to receive mandible in a position of rest; blade of mandible produced into a very slender hook which is almost straight, a little curved at extreme tip, at its base a very large, acute, flattened blade which is more than half length of mandible itself; in its angle this blade has a second, microscopic, tooth; prostheca with about five long, stout, comblike teeth exceeding the mandible in length, and an additional shorter, flattened blade marked with parallel grooves

lines. Maxilla with dense tufts of long yellow hairs; outer lobe produced cephalad as a hyaline, flattened blade which projects from prothoracic orifice when head is retracted.

Pupa.— Length, 8.5–9 mm.
Length of pronotal breathing horns, nearly 2 mm.
Width, d.-s., 1 mm.
Depth, d.-v., 1 mm.

Head, thorax, and appendages dark brown; pronotal breathing horns similar, but terminal half gradually paler, the tip almost yellow; abdomen pale brown.

Cephalic crest consisting of two prominent lobes, each with three strong setae, the most ventral directed outward; just before primary crest and lying between antennal bases, a very low, slightly bilobed crest which is not setiferous. Labrum elongate, obtusely rounded at apex and separating labial lobes, the latter produced caudally into subacute points. Maxillary palpi stout at base, narrowed to tip (Plate XLVII, 221). Antenna short (in female sex, at least), extending but a short distance beyond knee joints of fore legs. Pronotum (Plate XLVII, 220) high, feebly carinate medially. Breathing horns separated basally, very long and slender, sinuous, transversely wrinkled, at tip split into two flattened divergent lobes (Plate XLVII, 222 and 223). Mesonotum very short and convex, with numerous black dots which are most abundant anteriorly. Two small setae on either side behind wing axilla. Lateral angles of mesonotum blunt, but tip produced into a slender setiferous tubercle. Wing sheaths ending opposite tip of second abdominal segment. Leg sheaths short, ending just before tip of third abdominal segment, hind legs a little longer than others.

Abdomen with a narrow basal ring and a much broader posterior ring, the latter armed before posterior margin with a transverse row of small black spines, strongest on pleura, weakest on dorsum; on dorsum (Plate XLVII, 224) the spines reduced in number, there being from one to five (or in some cases none), and occurring only at or near ends of row; ends of row with two setae; on either side of median line a group of three closely approximated setae; usually segments 2 and 3 have the spines weak or lacking; segments 4 to 6 with two spines, and segment 7 with one spine, but in some specimens the number is slightly increased. Sternites (Plate XLVII, 225) with the intermediate segments (4 to 6) having about twenty spines in an almost continuous row which as a rule is uninterrupted; at each end of row about two strong setae; near base of posterior ring a narrow transverse area with two setae at each end. Pleura with a few powerful spines, small or lacking on basal segments, larger and more numerous on posterior segments, there being usually two on segment 4, three on segments 5 and 6, and four on segment 7; on pleura at about midlength of posterior ring and nearer dorsal side, three black setae in transverse alinement, these somewhat longer on basal segments; opposite basal ring a stout seta. Female cauda (Plate XLVII, 226) elongate; tergal valves slender, slightly upcurved, near apex with a sharp black spine which is directed dorsad, laterad, and caudad; two weak setae on either side before apex. Dorsum of segment 8 with four lobes; posterior pair elongate, slender, curved, and divergent; anterior pair blunt, small, and more approximated; just ventrad of these lobes a stout seta; pleural region with two powerful spines, above the more dorsal of which is a stout seta; a seta near ventral margin.

Nepionotype.— Ithaca, New York, May 30, 1917. No. 88–1917.
Neanotype.— With type larva, reared June 9, 1917.
Paratypes.— Larvae, May 30, 1917. Pupa, June 13, 1917.

Genus **Pilaria** Sintenis (Lat., derived from *the long antennal verticils*)

1888 *Pilaria* Sintenis. Sitzber. Nat.-Ges. Dorpat., vol. 8, p. 398.
1919 *Eulimnophila* Alex. Cornell Univ. Agr. Exp. Sta., Mem. 25, p. 917.

Larva.— Form moderately slender. Spiracular disk surrounded by four unequal lobes, lateral pair in some cases very reduced, elongate ventral lobes fringed with long hairs. Head capsule of Ulomorpha type. Mandible hinged, blade with one or two acute teeth at base. Maxilla densely hairy. Mentum not chitinized.

Pupa.— Pronotal breathing horns elongate-cylindrical, tips split into flattened lobes. Abdominal segments with three or four pairs of naked tubercles.

The genus Pilaria includes a group of species of the old genus Limnophila, comprising *Limnophila tenuipes* and *L. pilicornis* and their allies. Its relationships are plainly with Ulomorpha rather than with Limnophila. The genotype is *Limnophila pilicornis* (Zett.), of northern Europe. Other included species are *L. tenuipes*, *L. recondita*, *L. imbecilla* O. S., *L. edwardi* Alex., *L. quadrata*, *L. stanwoodae* Alex., and *L. osborni* Alex., of North America, and *L. discicollis* (Meig.), *L. fuscipennis* (Meig.), *L. subtincta* (Zett.), and probably other species, of Europe.

The immature stages are spent in mud or moist earth. In Europe, *Pilaria discicollis* (Plate XLVIII, 232) has been found by Gerbig (1913: 163–164) and by Cameron (1917:63). *P. fuscipennis* is described by Beling (1886:197–198) as living in mud near a ditch. Gerbig (1913:164–166) found the larvae (Plate XLVIII, 231) in a similar situation. Brauer (1883:54) describes them as living between decaying leaves in swamps. Cameron (1917:63) states that the larvae are found in decaying wood, this record possibly being an error. According to Beling, the pupal duration is not more than ten days. In America, *P. tenuipes* has been discussed by Hart (1898 [1895]:204–205) and by Malloch (1915–17b:223–224), as stated under the discussion of the species.

The species of the genus Pilaria may be separated by the following keys:

Larvae

Ventral lobes of spiracular disk elongate, heavily marked with brownish black; coloration pale yellow..*P. tenuipes* (Say) (p. 873)
Ventral lobes of spiracular disk short, pale; coloration deep yellow. *P. recondita* (O. S.) (p. 874)

Pupae

1. Pronotal breathing horns short, black; lobules of cephalic crest blunt and rounded. *P. quadrata* (O. S.) (p. 875)
   Pronotal breathing horns elongate, pale, brownish yellow or yellow; lobules of cephalic crest elongate, finger-like..2

2. Antennal sheaths of male elongate; pronotal breathing horns longer, pale yellow.
P. tenuipes (Say) (p. 873)
Antennal sheaths of male short; pronotal breathing horns shorter, yellowish brown.
P. recondita (O. S.) (p. 874)

Pilaria tenuipes (Say)

1823 *Limnobia tenuipes* Say. Journ. Acad. Nat. Sci. Phila., vol. 3, p. 21.
1869 *Limnophila tenuipes* O. S. Mon. Dipt. N. Amer., part 4, p. 210–211.

Pilaria tenuipes is a widely distributed crane-fly thruout eastern North America. The immature stages are commonly found in the mud of swamps, or near streams and other bodies of water. This is the unknown Limnophila described by Hart (1898 [1895]: 204–205), and also considered in much detail by Malloch (1915–17 b: 223–224), who found the pupae along the banks of the Sangamon River in Illinois.

Larva.— Length, 16 mm.
Diameter, 1.4–1.5 mm.

Coloration of living larva, pale brownish yellow. Body covered with a long, dark-colored, appressed pubescence, more conspicuous on posterior segments. Lateral pencils of setae near base and apex of segments. Antepenultimate segment of body capable of globular distention, covered with numerous transverse rows of microscopic roughened points. Spiracular disk (Plate XLVIII, 230) moderately large, surrounded by four lobes; ventral lobes long and slender, inner face with closely approximated, transverse, brownish black lines which cause entire face to appear dark; near tips of lobes these black marks tapering out into a long point; basal parts of dark marks subcontiguously hollowed out interiorly to form a large pale area below spiracles; ventral lobes fringed with long, pale hairs, some of them exceedingly elongate. Lateral lobes very small, blunt, tending to be reduced, bearing short fringes of dark hairs. Anal gills slender, pale in color.

Head capsule of Ulomorpha type and not very different from that of the type genus; dorsal plate broad basally, narrowed gradually behind to near tip where it expands into a very large spatula. Epipharyngeal region of labrum and maxillae fringed with dense tufts and brushes of long yellow hairs. Maxillary lobe relatively small but elongate, hyaline, tapering to flattened apex. Antenna (Plate XLVIII, 229) with basal segment elongate, bearing at its tip an elongate apical papilla which is a little longer than the segment, bluntly rounded at its tip, and delicately sculptured. Mandible (Plate XLVIII, 228) very long, hinged, at its base an acute tooth equal in length to about one-third length of mandible; in the type larva, the left mandible a little longer than the right mandible. Mental region not chitinized.

Pupa.— Length, 10–15 mm.
Width, d.-s., 1.5–1.6 mm.
Depth, d.-v., 1.6–1.8 mm.

Coloration dark brown; pronotal breathing horns light yellow, extreme bases brownish.
Cephalic crest small, composed of three slender, finger-like lobes which are tipped with strong setae; on front, before crest, two setiferous lobes. Labrum small, bluntly rounded

at apex. Labial lobes oval. Maxillary palpi slender. Antenna of female moderately elongated, reaching to just beyond wing root. Pronotal breathing horns (Plate XLIX, 233) elongate, cylindrical, sinuous, transversely wrinkled, apex scarcely enlarged but deeply split on inner margin; a setiferous tubercle ventrad and laterad of breathing horns. Thorax with a very high anterior median crest. A slender, setiferous tubercle above wing axil, and two others on either side of median line. Sheaths of halteres long and slender. Leg sheaths ending about on a level, or those of hind legs the shortest and those of fore legs a little longer.

Abdominal segments divided into two annuli. Tergites (Plate XLIX, 235) on posterior ring with a caudal row of blunt, naked tubercles; at end of row two setae; on either side of median area and just in front of row, a large setiferous tubercle; at base of ring two naked tubercles, one on either side of median line; two slender setiferous tubercles near margin of ring. Basal ring with four naked tubercles. (The third pair of tubercles found in the pupa of *Pilaria quadrata* is vestigial.) Pleura with four tubercles, two on each ring, the basal one of each ring setiferous, the posterior one naked. Sternites with six naked tubercles on basal ring, arranged in three transverse pairs; on posterior ring at base two setiferous tubercles, each with two bristles, directly behind last naked tubercle of basal ring; at caudal margin two or three large tubercles near end of row and about four or five small naked tubercles between. Female cauda (Plate XLIX, 234 and 236) very elongate, tergal valves slightly upcurved, terminating in a sharp spine and with two setae on outer face. Eighth tergite with four elongate lobes; posterior pair blunt, directed laterad; anterior pair elongate, slender, with two setae laterad of each. A blunt lobe on pleural region. Pleura with three or four powerful tubercles, with a seta located between the more dorsal pair. Sternal region with four small setae, two on either side of broad median area.

Nepionotype.— Orono, Maine, July 1, 1913. No. 50–1913.
Neanotype.— With type larva.

Pilaria recondita (O. S.)

1869 *Limnophila recondita* O. S. Mon. Dipt. N. Amer., part 4, p. 212–213.

Pilaria recondita is a common crane-fly thruout the northeastern United States. The immature stages are swamp inhabitants, and are very frequently found in exactly the same situations as are those of *P. tenuipes*. *P. recondita* belongs to the same group as *P. tenuipes*, and the pupae of the two species are very difficult to distinguish.

Larva.— Length, 15 mm.
Diameter, 1.2 mm.

Color a uniform light yellow.

Body covered with a long, appressed, yellow pubescence and with a few long setae. Spiracular disk very small, in a position of rest almost closed, surrounded by four lobes; ventral lobes moderately elongated, fringed with long, golden-yellow hairs which are longest at tips of lobes; if bent backward these elongate hairs extending to beyond gills; inner face of lobes almost unmarked, with only a delicate brown line extending from tip toward base

for a distance equal to about one-half length of lobes; lateral lobes small, subdorsal in position, separated by a narrow notch, their inner faces opposed to each other, margin fringed with short, golden-yellow hairs. Anal gills four, moderately elongated.

Head capsule as in *P. tenuipes*. Antenna with sculptured apical papilla tapering to blunt tip; besides this papilla, an even longer, hyaline, flattened blade. Mandible with apical bladelike part shorter and stouter, with two subequal stout triangular teeth at base (Plate XLVIII, 227).

Pupa.— Very similar to pupa of *P. tenuipes*, but smaller. Antennal sheaths of male short. Breathing horns a little shorter than in *P. tenuipes* but still much longer than in *P. quadrata*, of a pale yellowish brown color. On abdominal tergites, along caudal margin of posterior ring, from four to seven naked tubercles between the setiferous tubercles (in *P. tenuipes*, four or five). Male cauda (Plate L, 237) with dorsal lobes stout, cylindrical, narrowed at tips, divergent, directed caudad and ventrad; on outer face before tip a slender seta; ventral lobes blunt, with a flattened ventral tubercle at base of notch. Segment 8 on dorsum with posterior lobes blunt, straight, directed caudad and slightly laterad, but not so strongly as in *P. tenuipes*.

Nepionotype.— Orono, Maine, July 3, 1913.
Neanotype.— Ithaca, New York, emerged June 11, 1917. No. 112–1917.
Paratypes.— Pupa, Orono, Maine, placed in rearing as a fully grown larva, June 26, 1913; emerged as an adult male, July 3, 1913, showing a pupal duration of seven days. Larva, Orono, Maine, July 5, 1913 (No. 74–913).

Pilaria quadrata (O. S.)

1859 *Limnophila quadrata* O. S. Proc. Acad. Nat. Sci. Phila., p. 241.

Pilaria quadrata is a widely distributed spring and early summer species. The immature stages are very similar to those of *P. tenuipes* and *P. recondita*. A pupa was found by Dr. Needham in the Indian Spring, Ithaca, New York, where it was found floating among the water cress. From this pupa an adult female fly was reared. On June 3, 1917, the writer found two fully matured male pupae in Chickaree Woods near Ithaca. There had been a very heavy rainstorm on the preceding day, and the low spots in the woods had been converted into small ponds, many of the insects that normally live in the mud or beneath the decaying leaves being forced to the surface. The pupae of *P. quadrata*, as well as an abundance of Tipula larvae, were found clinging to small islands of débris floating on these temporary woodland pools. The adult flies emerged on June 3.

Pupa.— Length of cast pupal skin, 9–12 mm.

Coloration almost black, including pronotal breathing horns; abdomen more dusky gray.

Cephalic crest small, black, trilobed, each lobe with a seta at apex. Labrum narrow, blunt at tip. Labial lobes rounded. Sheaths of maxillary palpi elongate, tapering to the

slender points. Antenna short in both sexes. Pronotal breathing horns (Plate L, 238) moderately elongate, cylindrical, transversely wrinkled, at tips smooth, flattened, and slightly enlarged. A tubercle with two long setae above wing axil. Two setiferous punctures on dorsum on either side of median line. Wing sheaths ending before tip of second abdominal segment. Leg sheaths ending before tip of third abdominal segment, the tarsal sheaths ending about on a level or the hind legs shorter.

Abdominal segments with tergites (Plate L, 239) 2 to 6 provided with eight naked discal tubercles, arranged in four transverse pairs, the third pair more approximated; laterad of third pair of naked tubercles, two small setiferous tubercles; on seventh segment one of the four pairs of tubercles lacking; near caudal margin of segments a transverse row of weak setiferous tubercles; on either side of median line, in alinement with discal tubercles and just anterior to the transverse setiferous row, a large tubercle provided with three setae. Pleural region carinate, each segment armed with four slightly curved tubercles: anterior one solitary, setiferous; second one solitary, naked; third one with two or three setae; posterior one bifid, naked. Sternites (Plate L, 240) with six naked, discal tubercles corresponding to those of tergites but reduced in number. Subterminal armature weak, ends of rows tuberculate; an isolated setiferous tubercle ventrad and laterad of ends of rows. Male cauda (Plate L, 242) elongate; dorsal lobes elongate-cylindrical, directed caudad and slightly dorsad, tapering to acute tips; three weak setae on outer ventral face; ventral lobes blunt, much shorter than dorsal lobes, with a blunt median lobule between them at their base; eighth segment on tergum provided with a large, blunt, median tubercle, with two large posterior lobes which are directed caudad and with two tiny lobes on either side in front; sternum with a transverse row of four separated setiferous tubercles; caudal margin with a transverse row of about eight or nine pale tubercles on either side, the outermost the largest; a small seta above second tubercle at ends of row. Female cauda (Plate L, 241) very long and slender, subacicular, sternal valves a little shorter than tergal valves; tergal valves terminating in blunt cylindrical points.

Neanotype.— Male pupal skin, Ithaca, New York, June 3, 1917.
Paratypes.— Pupa, a male skin with type pupa; a female skin, Ithaca.

Subtribe **Hexatomaria**

The subtribe Hexatomaria comprises a well-defined division with but four known genera, three of which are North American and are considered in this paper. The only other group of crane-flies with which the species may be confused are certain of the Limnophilaria, especially the Ulomorpha group of genera.

The larvae have the labral sclerite of the head capsule large, separated from the remainder of the capsule by a distinct suture. The epipharyngeal region is restricted to the anterior median part of the sclerite, and is provided with two large tubercles on either side, which are tipped with two or three hyaline, cylindrical papillae. Between these papillae is a brush

of hairs surrounding two pairs of setiferous tubercles. The mental region is not chitinized. The dorsal plates of the head capsule are widely separated from each other by a median split.

The pupae are often armed with spines or tubercles on or about the head and the thorax. The lateral abdominal spiracles are large and functional.

The genera of the subtribe Hexatomaria may be separated by the following keys:

Larvae

1. Coloration of body a deep saturated orange-yellow; spiracular disk with ventral lobes unlined with darker, bearing at tips a few very long hairs... *Penthoptera* Schin. (p. 891)
   Coloration of body pale yellow, whitish, or greenish; spiracular disk with lobes lined with dark brown or black.......................2
2. Size small, form slender (length 14–15 mm., diameter 1–1.3 mm.)..*Hexatoma* Latr. (p. 877)
   Size larger, form stouter (length over 15 mm., diameter over 1.6 mm.) *Eriocera* Macq. (p. 881)

Pupae

1. Pronotal breathing horns short and stout, red at base and apex, the remaining part dark-colored, transversely wrinkled; horns bent strongly toward each other at tips. *Penthoptera* Schin. (p. 891)
   Pronotal breathing horns not as above.......................2
2. Size small (length under 10 mm.).......................*Hexatoma* Latr. (p. 877)
   Size larger (length over 12 mm.).......................*Eriocera* Macq. (p. 881)

Genus **Hexatoma** Latreille (Gr. *six* + *I cut*)

1809 *Hexatoma* Latr. Gen. Crust. et Ins., vol. 4, p. 260.
1818 *Nematocera* Meig. Syst. Beschr. Zweifl. Ins., vol. 1, p. 209.
1818 *Anisomera* Meig. Syst. Beschr. Zweifl. Ins., vol. 1, p. 210.

Larva.— Size small (length of *Hexatoma megacera* about 14 mm.). Spiracular disk surrounded by two pairs of lobes, ventral pair the longer, inner face marked with a narrow brown line which is expanded at its inner end. Head capsule with lateral angles of labrum elongate and densely clothed with hairs.

Pupa.— Size small (length under 10 mm.). A large spinous tubercle on scape of antenna. No median projection on mesonotal scutellum. Pronotal breathing horns short and straight. Wing pads with cell R_2 very small and M with but a single branch reaching wing margin.

The genus Hexatoma includes a small number of forms with a chiefly Holarctic distribution, there being about eleven Palearctic, two Ethiopian, and one North American species so far described. The adult flies of the North American species, *Hexatoma megacera*, are common on vegetation along the banks of rather large streams. They are discussed herein in detail under the account of this species. The adult flies of some of the larger European species have habits quite like those of the genus Eriocera,

as discussed elsewhere in this paper (page 705). Riedel (1909:29) describes in some detail the habits and swarming of *H. bicolor* (Meig.), the males of which are very active in the forenoon during the hours of brightest sunlight, the females resting on the willow branches near by. Similar habits are recorded by Riedel (1910:30) for *H. saxonum* (Lw.). The immature stages of the European species are practically unknown, the only original reference being that of Von Röser (1834), who states that the larvae of *H. nigra* Latr. live in the sand along the banks of streams.

Hexatoma megacera (O. S.)

1859 *Anisomera megacera* O. S. Proc. Acad. Nat. Sci. Phila., p. 242.

The adult flies of *Hexatoma megacera* are on the wing during the months of May and June and may be swept from the rank vegetation along the streams from which their larvae emerged. The following notes on copulation, resting positions, egg laying in nature and in captivity, and other details, are quoted from published field observations (Alexander, 1915 c: 143–145):

May 14, 1911 — This usually rare insect was common on a grassy plot of land along Cascadilla Creek [Ithaca, New York]. The flies sit on the blades of grass, the long antennae of the male directed straight ahead. The males are very poor fliers and prefer to drop to the ground when disturbed and clumsily work their way off along the ground. When approached from the side they are much more easily alarmed and fly away. When approached from above, they do not move until the stick, finger, or whatnot, is within a couple of inches when they remove the fore feet from the support and, on nearer approach, fall to the ground When in copulation, the female tries to disengage by rapidly vibrating the wings in attempted flight, repeating this often, from every one to five seconds until disengaged or exhausted The male can disconnect himself at will. In copulation the female is always uppermost unless exhausted, when both sexes lie flat on a grass-blade. The female has the head up the male the head downward; copulation always takes place on a vertical support, usually a blade of grass, sometimes a plant stem. The sexes remain in copulation for quite a long time and are perfectly motionless. All of the legs of both sexes are on the support unless in a position where this is physically impossible, in which case as many as possible are used the hind legs of both sexes are held at right angles to the support, the forelegs in front. After copulation the female generally drops to the ground, the male, after a few moments' rest, flies away. Specimens in copulation were found in abundance from 2 to 4.30 p.m. when no more could be discovered. From 4.30 to 7 p.m. solitary males were common, but no females could be found on the grass-blades. At 4.30 p.m., a few females were found clinging to the trunk of the willow trees about two feet from the ground. At 5.30 p.m., females were noted in small groups over the water, evidently engaged in oviposition, as they frequently dipped down to the surface. These latter were in company with a large swarm of dancing empidid flies (Rhamphomyia). Of the great numbers that were picked from grasses in the afternoon a considerable proportion were females and toward 5 p.m. they commenced egg-laying on the sides of the containing vessel, large shell vials. By 7 p.m. the sides of the vials were black in places with the large, dark-colored eggs. This data would seem to place the time for oviposition at about sunset. The females are very good fliers and often travel for lon

distances before alighting as is shown toward sunset when they fly for long stretches up-stream. The males are rather poor fliers, due in part, possibly, to the weight of the long antennae and, as stated before, this sex prefers to skulk rather than fly. When the males fly, they do so heavily and seize the first support that they collide with and hang on, occasionally flying on immediately to another support. When the male comes in contact with a stem, he very often ascends to the top by means of a part-flying, part-climbing motion and, on reaching the summit, flies off to another place. As a rule the flies, especially the females, alight on a single grassblade, but very often the males are observed on two blades, the legs of one side on one blade and those of the opposite side on the other; when the body thus hangs between the stalks, the tarsi diverge from one another, whereas on a single support, the legs converge.

Hexatoma was preyed upon by large numbers of a scatophagid fly that occurred in great abundance in this vicinity and seemed to be subsisting almost entirely on these flies. At least twenty of these predaceous flies were noted with Hexatomae and this species seemed to constitute the principle insect enemy of the crane-fly. They would lurk on the grass blades and sally forth after their prey, carrying it back to some point to feed upon it. It is probable that the blood is taken since the body of the Hexatoma appeared almost uninjured when examined. On an old beam where males had a habit of walking up the vertical face, a small spider's web was found, in which eleven specimens were entangled, two being still alive; eight of these were males, the remaining three, females.

The males especially can walk up smooth surfaces, as glass, moving the legs alternately and awkwardly. The first pair taken were in copulation but in placing them in the vial they became disengaged and ran about in the container. After a short time they began to copulate in the tube.

May 15, 1911 — A pair were taken in copulation at 10 a.m.; at 8 p.m. they were still in coitu, but this is exceptional as most of the pairs disengage very readily. In the morning the species is very active and although the males do not fly far, they fly readily and it is difficult to pick them up by hand. The females are excellent fliers especially in the morning.

Several pairs were taken in copulation and each pair was isolated in a separate vial in order to ascertain the number of eggs per female. The clutch was determined by dissection. When the captive insects began to oviposit, the eggs shot out from the body, at first slowly, then more rapidly, one per second, later much slower again, the eggs being extruded one at a time. The total period of oviposition required seven minutes; at the end of sixty seconds, in the space between sixty and seventy seconds, eighteen eggs were laid, or 1.8 per second. Toward the end of egg-laying, the eggs appeared much more slowly, one in two seconds. The eggs are quite sticky or viscid and adhere to the glass. When the female is in danger of death, as when she falls into the water, she begins, at once, to deposit the egg-complement. In nature it seems probable that one egg is laid at each descent to the water. As soon as the female touches the water, although she has not deposited an egg all day, she immediately starts to deposit the oblong black eggs. After the last egg is expelled the muscles of the ovipositor still go through the motions of expulsion. One specimen was placed in the water and as usual began to deposit her eggs. She was decapitated, laid eleven eggs and tried to lay still more but failed. The number of eggs laid varied from 316 to 372 with an average of 347; the time required for oviposition varied from seven minutes to seven minutes and forty seconds. In most cases the number of the egg-complement is probably between 300 and 400.

The greater part of the larval existence is probably spent in the water, and it is only when the larvae are fully grown and ready to pupate that they come to land. On April 26, 1914, gravel from the bank of Cascadilla Creek was carefully examined, but no signs of larvae or pupae were to be discovered. On May 6, however, the same bank was examined and about ten larvae and seventy-five pupae were found. Sometimes the immature stages are very abundant. On May 12, 1917, near the place

just described, the writer found larvae and newly transformed pupae in great numbers, the former pupating in the dry sand rather distant from the water's edge. In one dry patch of sand on a rocky ledge, sixty specimens were found in six square inches of soil. The insects are often found in gravel or coarse sand that is thickly penetrated by grass roots and rhizomes, rarely in pure gravel. They are most commonly found in soil that has been recently deposited after freshets. The immature stages of Hexatoma are associated with larvae of *Eriocera spinosa*, *E. cinerea*, *Tipula bella*, and *Atherix* probably *variegata* Walk., with pupae of *Chrysops excitans* Walk., and with many beetles such as *Paederus littorarius* Grav., *Gastrolobium bicolor* (Grav.), *Bledius* sp., *Omophron* sp., *Dyschirius sphaericollis* Say, *Tachistodes partiarius* (Say), *Anadaptus discoideus* (Dej.), *Laccobius agilis* Rand, and other species characteristic of the sandy margins of large streams. The pupal duration of Hexatoma is six and one-half days.

Larva.— Length, 14–15 mm.
Diameter, 1–1.3 mm.

Color of body, pale brownish yellow.

Body covered with rather abundant appressed hairs, the subterminal distended part of abdomen with transverse rows of very short spines or setae, there being from thirty-five to forty such rows. Spiracular disk (Plate LI, 246) surrounded by four lobes; ventral lobes the longer, with a fringe of a few long hairs at apex; on inner face a long, narrow, brown mark, extending from the tip inward, the proximal end expanded; lateral lobes with numerous long hairs which are gradually shorter toward base of lobes. Spiracles circular, situated at base of lateral lobes; a dusky mark extending from spiracles dorsad.

Head capsule of usual hexatomine type, as described for *Eriocera longicornis* (page 888). Entire general features and details of mouth parts very similar to those of *Eriocera longicornis*. Labrum (Plate LI, 243) transversely oval, with frame strong and chitinized, anterior median part produced into a small lobe (Plate LII, 250) bearing two lateral papillae and two setiferous tubercles surrounded by short hairs; lateral margins of labrum produced into prominent lobes directed proximad and cephalad, densely hairy and entirely protecting anterior margi of labrum. Antenna (Plate LI, 244) with apical papillae shorter than segment, the larges papilla transversely sculptured (Plate LII, 251). Mandible (Plate LI, 245) long and slen-der, the lateral teeth more accentuated than in Eriocera; largest tooth with a flattened trun-cated blade in its axil, this in some cases broken up into two or three small blades; basa of largest lateral tooth a flattened lobe which is barely indicated in the species of Eriocer studied. Maxilla with outer flattened blade conspicuous; palpus near its base on inne side, similar to the condition obtaining in Eriocera; just laterad of palpus a powerful seta

Pupa.— Length, 9.2–9.6 mm.
Width, d.-s., 1.2 mm.
Depth, d.-v., 1.4 mm.

Pupa (Plate LI, 247) very similar to that of *Eriocera longicornis*, differing only in its small size, greater development of scapal spine, lack of projection on mesonotal prescutum, and a few lesser characters. Cephalic crest (Plate LI, 248 and 249) as viewed from beneath, very different in shape. Fore pair of legs much shorter than the others, ending just beyond posterior margin of second abdominal segment; hind pair of legs extending far beyond the others, ending beyond midlength of third abdominal segment; in some specimens the tarsal segments much closer to posterior margin of third abdominal segment, but usually a marked difference in tips of tarsi of the various legs. Cephalic crest as viewed from side, triangular, ending in an acute point directed strongly forward. Viewed from beneath, lobes conspicuously triangular, pointed, lying parallel or slightly divergent and separated by a deep median split. Spine on scape of antennae very large, conspicuous. Tubercle on labrum strongly developed. Antennal sheaths of male very long, those of female much shorter. Pronotal breathing horns short, straight. Mesonotum strongly wrinkled along median line; scutellar lobe not developed. Wing pads dark, venation not showing clearly but, if made out, the very short cell R_2 and the reduced M characteristic of Hexatoma alone. Posterior leg sheaths extending beyond level of middle legs, these, in turn, being longer than sheaths of fore legs.

Abdomen (Plate LII, 252) with about thirty-four spicules on sternite 4, about thirty in a straight, uninterrupted row on tergites 3 and 4, and about twenty on tergite 5. Chaetotaxy about as in *Eriocera longicornis*, but the seta lying ventrad of spiracle on pleurites much farther ventrad and very weak. Male cauda with sternal lobes strongly rounded, enlarged, and bent suddenly dorsad. Female cauda as that of male; ovipositor viewed from side with an obtuse notch; from beneath, sternite obtusely pointed and with a deep median split; from above, tergite almost flat across caudal margin, the lateral angles rounded, with a deep median split.

Nepionotype.— Ithaca, New York, May 6, 1914.
Neanotype.— Type locality, May 2, 1913.
Paratypes.— Several hundred larvae and pupae from type locality.

Genus **Eriocera** Macquart (Gr. *wool* + *horn*)

1830 *Caloptera* Guér. Voyage de la Coquille, Zool., Ins., pl. 20, fig. 2.
1838 *Eriocera* Macq. Dipt. Exot., vol. 1, p. 74.
1838 *Evanioptera* Guér. Voyage de la Coquille, Zool., vol. 2, part 2, p. 287.
1848 *Pterocosmus* Walk. List Dipt. Brit. Mus., vol. 1, p. 78.
1850 *Allarithmia* Loew. Bernstein und Bernsteinfauna, p. 38.
1857 *Oligomera* Dolesch. Natuurk. Tijdschr. Nederl. Indie, vol. 14, p. 387.
1859 *Arrhenica* O. S. Proc. Acad. Nat. Sci. Phila., p. 242.
1859 *Physecrania* Bigot. Ann. Soc. Ent. France, ser. 3, vol. 7, p. 123, pl. 3, fig. 1.
1912 *Androclosma* Enderlein. Zool. Jahrb., vol. 32, part 1, p. 34.
1916 *Globericera* Matsumura. Thous. Ins. Japan, add. 2, p. 471.

Larva.— Spiracular disk surrounded by four lobes which are rarely (as in *Eriocera cinerea*) subobsolete, inner face lined with brown or black, tips with fringes of moderately long hairs. Head capsule long, narrow, the constituent plates very slender; dorsal plate completely divided tho contiguous or approximated behind. Labral sclerite large and conspicuous, sensory tubercles and papillae crowded on median cephalic region. Mandible long, acute

at tip, with two teeth at about midlength. Maxilla with outer lobe greatly prolonged into a flattened blade. Antenna cylindrical or clavate, with three or four long papillae at tip. Mentum not chitinized, in *E. cinerea* with a flattened rectangular plate on either side, this armed with numerous hooks and spines.

Pupa.— Cephalic crest of various shapes and sizes, very reduced in *Eriocera spinosa*. Antennal sheaths of males of several species (*E. spinosa*, *E. longicornis*, *E. cinerea*) very long, extending beyond end of wing pad. Pronotal breathing horns of various shapes, acutely pointed in *E. spinosa*, short and blunt in several species. Head and thorax often with spines or tubercles on scape of antenna, on labrum, or (in *E. spinosa*) on face of eye; a tubercle on scutellum (in *E. longicornis*), one on dorsum of second abdominal segment (in *E. spinosa*). Abdominal segments with a conspicuous transverse armature of spines near posterior margin. Lateral spiracles large, distinct.

Eriocera is an extensive genus (including approximately 150 species) of medium-sized to large flies, most of which are tropical. The genus has not been found in Europe, but elsewhere it is represented by a host of species. The habits of the adult flies have already been noted (page 704). The immature stages are spent in sand or gravel near running water, more especially along large streams. A more complete account of the genus is given by Alexander and Lloyd (1914) and by Alexander (1915 c: 148–152).

The occurrence of the flies is somewhat local. During an entire summer of collecting in Maine in 1913, the writer did not find a single specimen of any species; and Dr. Dietz has stated that the only living individual which he has found was a single male of *Eriocera spinosa* taken in the Pocono Mountains in Pennsylvania. On the other hand, the flies are often found in countless numbers, and several species may be found associated together. Thus, at Ithaca, New York, in the sandy gravel along Cascadilla Creek, the immature stages of four species of Eriocera and one of the closely related Hexatoma occur together in unlimited numbers.

The species of Eriocera may be separated by the following keys:

Larvae

1. Lobes surrounding spiracular disk obsolete or nearly so; a flat, chitinized plate with serrate margins on either side of mental region . . . . *E. cinerea* Alex. (p. 886)
   Spiracular disk surrounded by four slender lobes; no plate as described above on mental region 2
2. Very large (length 40–45 mm., diameter 4–5 mm.); spiracular disk with ventral lobes narrowly lined with black, inner ends of each forked, Y-shaped; lateral lobes narrowly lined with black, inner ends of marks expanded . . . . *E. spinosa* (O. S.) (p. 883)
   Smaller (length under 30 mm., diameter under 2.5 mm.); spiracular disk not marked as above 3

. Ventral lobes of spiracular disk bearing one or two very long, dark setae in addition to the shorter yellowish fringe; inner face of each lobe with a capillary black line which is suddenly expanded at its inner end into a triangular brown mark, the two marks inclosing an oval pale area between their proximal ends; lateral lobes with a capillary black line. . . . . *E. fultonensis* Alex. (p. 890)
Ventral lobes of spiracular disk with apical fringe consisting of numerous long, pale setae; inner face of each lobe lined with pale brown, at about midlength gradually expanded into an elongate-triangular mark, the two marks inclosing a linear pale area between their proximal ends; lateral lobes with a brown line. . . . . *E. longicornis* (Walk.) (p. 888)

Pupae

. Size large (length 25 mm. or over); pronotal breathing horns tapering to acute tips; cephalic crest small, reduced to four small tubercles; cell M_1 on wing pad present; a strong spinous tubercle on either side of median line at base of second abdominal tergite; a tubercle on eye. . . . . *E. spinosa* (O. S.) (p. 883)
Size smaller (length under 18 mm.); pronotal breathing horns blunt at tips; cephalic crest prominent; cell M_1 on wing pad lacking; no tubercles on second abdominal tergite or on eye. 2
A tubercle on mesonotal scutellum. . . . . *E. longicornis* (Walk.) (p. 888)
No tubercle on mesonotal scutellum. 3
Pleurites of abdominal segments with a transverse row of three setae ventrad and slightly caudad of spiracle; antennae of male elongated. . . . . *E. cinerea* Alex. (p. 886)
Pleurites of abdominal segments with two stout setae dorsad and caudad of spiracle; antennae short in both sexes. . . . . *E. fultonensis* Alex. (p. 890)

riocera spinosa (O. S.)

1859 *Arrhenica spinosa* O. S. Proc. Acad. Nat. Sci. Phila., p. 244.
1869 *Eriocera spinosa* O. S. Mon. Dipt. N. Amer., part 4, p. 252–253.

Eriocera spinosa is the commonest of the large species of the genus eastern North America. The larvae occur in great numbers beneath cks in rapid water in the autumn, when they form a considerable proortion of the insect life in the streams. When about to pupate they go the neighboring banks and live for some time in the sand or gravel. he habits of the larvae have been discussed by Alexander and Lloyd 914:16–17) and by Alexander (1915c:149).

The larvae were found on May 1, 1913, along the banks of Fall Creek, haca, New York, in considerable numbers. They were associated with ung and mature pupae of *E. longicornis*, which were emerging in great umbers at the time. On May 27, both larvae and pupae of *E. spinosa* ere found to be very abundant, the larvae being more numerous in the etter places, the pupae in the drier spots. They occurred at various stances from the water's edge, from within a foot of the margin to as r back as eight or ten feet. The pupae are found in short, more or less rtical, burrows, from one to three inches below the surface. Not often

were larvae and pupae found in close proximity to each other. Pupa of *E. spinosa,* as well as of all other species of the tribe as known, ar very active when removed from their burrows, wriggling rapidly to an fro, and are exceedingly tenacious of life. Larvae, as found on Ma 27, were mostly contracted; a few, however, were expanded and had th subterminal segment of the abdomen swollen. In this regard it may b mentioned that almost all of the larvae of crane-flies that live in the san or mud along the banks of streams have this ability to inflate the en of the abdomen. Larvae of Eriopterini, of Pediciini, and of Hexatomir have been observed with this conspicuous enlargement. It is undoubtedl used to propel the larva thru the soil by alternate expansion and cor traction of the segment.

Larvae of *E. spinosa* were placed in breeding jars on May 13 and adul flies emerged on the 28th. It is probable that the pupal stage is no longer than from ten to twelve days, at the most. On May 30 a larg number of larvae and pupae were brought into the laboratory in a bucke of gravel. Some of the fully matured pupae transformed in the pa while being brought to the laboratory.

The larvae are carnivorous. Their powerful, sickle-shaped mandible are capable of inflicting a painful bite on tender parts of the hand. S. C Rich placed larvae in dishes together with the nymphs of various drago flies. The smaller of the nymphs were eaten by the Eriocera larvae, thu confirming previous observations on the carnivorous habits of the specie

Larva.— Length when fully extended, 40–45 mm.
Diameter, 4–5 mm.

Color varying from very pale whitish to rather dark brown; in life, the skin showir conspicuous bronzy reflections.

Spiracular disk (Plate LIV, 262) surrounded by four slender elongate lobes, one pair beir lateral, the other ventral, in position; inner face of lateral lobes with a capillary black lin this beginning as an enlarged black spot just ventrad of spiracle, reaching tip of lobe; dors outer edge of lobe with a dense fringe of long, conspicuous, reddish hairs, inner edge of ro beginning just laterad of spiracle where the hairs are very short, gradually becoming long to tip, where they are as long as the lobe itself; ventral lobe with a capillary black line c proximal edge, this dividing at base of lobe, the lower branch running along ventral marg of stigmal field and approaching its fellow of the opposite side on median line of body; dense fringe of conspicuous reddish hairs at tip of lobe and continued on outer dorsal si for a short distance toward base; a few dusky brown spots on stigmal field between spiracl two small hairs between spiracles. Spiracles rather small, widely separated. Undernea caudal lobes and behind penultimate swollen segment, four anal gills, short, stout, cylindric

the lateral pair directed outward, the inner pair directed caudad. Head capsule (Plate LIV, 267) broad in proportion to its length, measuring 3.5–3.8 mm. by 1.8–2 mm. (across dorsal plates). Papillae at tip of antenna short, not more than one-third length of segment. Mandible (Plate LIV, 271) lacking a prominent conical tooth at midlength, such as is found in *E. cinerea* and other species.

Pupa.— Length: male, 26.5–27 mm.; female, 25–28.5 mm.
Width, d.-s.: male, 3.4–3.9 mm.; female, 3.4–4 mm.
Depth, d.-v.: male, 4–4.2 mm.; female, 3.5–4 mm.

In life, pupae varying in color from very pale yellowish to dark brown or almost black, the deepest color being that of head and thorax of old pupae; body often showing bronzy reflections.

Cephalic crest very reduced, scarcely projecting beyond level of antennae; viewed from beneath, somewhat quadrate, the anterior lateral angles produced into small pointed lobes bearing a small seta at apex; viewed from side a second pair of lobes is seen, these being subequal to anterior lobes in size, and likewise setiferous. Spine of antennal scape very large, somewhat curved, directed ventrad. Inner caudal surface of eye with a conspicuous tubercle. Tentorial region produced into a small median tubercle. Tubercles at base of labrum very large, close together, their tips strongly chitinized; a small seta above each of these labral tubercles and another small seta on each cheek. Pronotal breathing horns long, slender, broad at base, flattened and rather pointed at tips, the organ arcuated so that apex is bent strongly ventrad. Mesonotal scutellar lobe (Plate LV, 280) prominent, rather strongly projecting. Wing pad light brown, venation showing very clearly, the presence of cell M_1 in connection with elongate antennae in male sex being found in this species alone in eastern North America. Leg sheaths with tarsal sheaths ending on a level, about opposite end of third abdominal segment.

Second abdominal tergite with a conspicuous basal tubercle on either side of median line. Abdominal segments (Plate LVI, 283) with subterminal rows of spines, there being about twenty to twenty-two on tergites 2 to 5; tergites 6 and 7 destitute of spines but with four subapical setiferous tubercles; tergites 2 to 7 with a conspicuous setiferous tubercle on ventro-cephalic angle of each posterior ring; eighth tergite concave on posterior margin, bearing a pair of strong apical tubercles on either side of median line. Pleural region of abdomen rather restricted, longitudinally wrinkled. Spiracles large, elliptical, transverse, placed about opposite midlength of segments. Three small setiferous tubercles ventrad and caudad of spiracle, and another similar tubercle on dorso-cephalic angle of each pleuron. Sternites on segment 3 with two spines on each outer angle; segments 4 to 6 with from sixteen to twenty spines; segment 7 with about ten spines; an isolated setiferous tubercle caudad and dorsad of ends of row; segments 4 to 7 with a setiferous tubercle about midlength of posterior ring; segment 8 lacking soft pleural region, bearing an apical row of strong spines which are interrupted only on dorsum and for a small space on median line of venter, there being about twenty of these spines in the circlet. Male cauda (Plate LV, 281 and 282) with ninth sternite rounded, swollen, with a deep median furrow bearing a small lobe on ventral side at end of split; ninth tergite produced caudad into two strong conical points separated by a V-shaped notch, these points directed caudad and slightly dorsad, each one a little split near tip on outer face and with a prominent lateral tooth at about midlength. Female cauda (Plate

LVI, 284) with ninth sternite elongated, cylindrical, its tip rounded, feebly split beneath; ninth tergite very long, pointed, with a deep median split.

Nepionotype.— Ithaca, New York, May 1, 1913.
Neanotype.— With type larva.
Paratypes.— Numerous larvae and pupae with types, May 1–15, 1913.

Eriocera cinerea Alex.

1912 *Eriocera cinerea* Alex. Psyche, vol. 19, p. 169–170, pl. 13, fig. 9.

Eriocera cinerea is locally common, flying in May. The larvae were found on May 16, 1917, in sand along the banks of Cascadilla Creek, Ithaca, New York. They have been found at various dates during the past few years, but always in scanty numbers. Larvae found on April 28 were associated with larvae of *Hexatoma megacera, Eriocera spinosa*, Atherix, and other insects. The larvae are stouter than those of *E. longicornis* and are pale whitish yellow, quite devoid of the greenish tints of the latter species. A larva found on April 28 transformed to an adult female on May 16. Additional larvae and pupae were found on May 24, and a few pupae on May 30, 1917.

The supposed larva of *E. longicornis* described by Alexander and Lloyd (1914:21–23) pertains to this species; the true *longicornis* is discussed later in this paper.

Larva.— Length, 15–16 mm.
Diameter, 2–2.2 mm.

Color light yellow.

Form almost terete, abdominal segments subdivided into two annuli. Subterminal abdominal segment greatly enlarged, capable of great distention. Spiracular disk (Plate LIV, 263 and 264) very reduced, the usual four lobes exceedingly small; ventral lobes practically obsolete, not projecting, each fringed with from twenty to thirty long, golden-yellow hairs; lateral lobes very short, triangular, fringed with from twelve to fifteen long hairs; a faint dusky mark from dorsal margin of each spiracle to edge of field; a faint vertical stripe between spiracles; ventral lobes marked with brownish black, the mark of each side three-pointed at its inner end, the innermost of these points connected with its fellow of the opposite side; lateral lobes with the marks elongate, triangular, the points directed outward. Spiracles small, oval, separated by a distance a little less than the diameter of one. Anal gills four, very short and inconspicuous.

Head capsule long and narrow, measuring about 1.5 by 0.275 mm.; dorsal plates of capsule with proximal anterior angles produced inward. Labral sclerite (Plate LII, 253) having labrum itself subquadrate. Mental region entirely lacking strongly chitinized points as in this group of genera. Present species showing a structure which is probably a part of labium, either mentum or hypopharynx, and which has not been found in any other species of the

genus (Plate LII, 254); this structure located on either side of capsule on ventral face, a flattened, subrectangular plate whose surface, except at base, is densely set with small spines and large pits; inner margin provided with large, acute spines, beginning at about one-third length of sclerite, gradually enlarged toward tip, at inner angle acute; these teeth interrupted before outer posterior angle, which terminates in a blunt, flattened lobe. Antenna cylindrical, apex obliquely truncated, terminating in a slender apical papilla which is longer than the segment that bears it, broad at base, tapering gradually to tip; two or three long apical setae; small auditory plates at about one-third length of segment. Mandible (Plate LII, 255) a powerful, slender, curved hook, at about midlength with a strong pointed tooth bearing in its axil a smaller tooth; as is usual in the genus, an egg-shaped chitinized piece isolated in one of the ventral tendons of mandible. Maxilla arising just ventrad of mandible, outer lobe persisting as a very elongate, bladelike organ.

Pupa.— Length, 13–15 mm.
Width, d.-s., 1.6 mm.
Depth, d.-v., 1.7 mm.

Head and appendages dark brown, thoracic dorsum a little paler; abdomen with posterior rings of tergum and sternum dark brown, producing a banded appearance.

Cephalic crest (Plate LIII, 257) very large and conspicuous, consisting of two rounded lobes behind, each tipped with a strong seta; anterior part of crest directed ventrad and consisting of two lobes, the larger bearing a strong seta on outer face; viewed from front, these anterior lobes separated by a very narrow, U-shaped, median notch; crest of female a little smaller. Two blunt tubercles on scapal segments of each antenna. Junction of clypeus and labrum with two tubercles, above and slightly laterad of each a strong seta. A strong seta on cheek below eye. Labrum broad, very obtusely rounded at tip. Labial lobes rectangular, widely separated. Maxillary palpi blunt at tips (Plate LIII, 258). Antenna of male elongate, exceeding wing and ending opposite base of last tarsal segment of hind leg. Pronotal breathing horns short, slender, cylindrical, scarcely longer than cephalic crest. Two long curved setae and a smaller straight seta laterad and ventrad of base of each breathing horn. Lateral angle of thorax with two setae; two long setae above wing axil (Plate LIII, 256). A strong seta on either side of mesonotum and a group of two small setae in front of each of these. Wing sheaths extending to base of third abdominal segment. Leg sheaths extending to base of fourth abdominal segment; tarsal sheaths ending about on a level, or those of fore legs considerably shorter.

Abdominal segments (Plate LIII, 259) divided into two subequal rings. Chaetotaxy as follows: pleura with a seta on dorsal margin of basal ring; a transverse row of three setae on posterior ring, lying ventrad and slightly caudad of spiracle (as in *E. spinosa*); tergum with basal ring unarmed, posterior ring with a subterminal row of sharp black spines; two long setae at each end of row and a few small setae at intervals along row; a solitary seta on basal lateral part of posterior ring; armature weaker on posterior segments, on segment 7 being reduced to four separated groups of setae, the outer groups with a single spine; sternum with basal ring unarmed, posterior ring with a subterminal transverse row of stout black spines with two long setae at each end of row and an isolated seta laterad and caudad of end of row; at base of ring on either side a group of two setae, the lateral one the smaller. Male cauda (Plate LIII, 260) with the sharp dorsal lobes directed dorsad, rather acute at tips, two

setae on outer face before tips; viewed from above, these setae seen to be separated by a deep U-shaped notch; eighth segment with a dorsal pentagon of five closely approximated lobes; just laterad of these a group of three setae, the posterior one long and slender, the anterior one short and stout; pleural region produced into a long lobe tipped with a slender seta; on sternum two small setae on either side. Female cauda (Plate LIII, 261) elongate, tergal valves very long and slender, two delicate setae on either side before tip and a stouter one at tip.

Nepionotype.— Ithaca, New York, April 28, 1917.
Neanotype.— Fall Creek, Ithaca, May 18, 1917
Paratypes.— Larvae and pupae with types.

Eriocera longicornis (Walk.)

1848 *Anisomera longicornis* Walk. List Dipt. Brit. Mus., vol. 1, p. 82.
1869 *Eriocera longicornis* O. S. Mon. Dipt. N. Amer., part 4, p. 253–254.

Eriocera longicornis is probably the commonest species of the genus in the eastern United States. The adult flies are sometimes very abundant, occurring in swarms in late afternoon and early evening in May, some of the swarms numbering thousands of individuals. At other times of the day, the flies may be found resting quietly on bushes. The larvae live in the sand near the water's edge. The pupal duration is seven days. The detailed life history of this species is given on pages 704 to 708.

Larva.— Length, 17–19 mm.
Diameter, 2–2.3 mm.

Color, greenish brown.

Body covered with a long, appressed, dark pubescence. Penultimate segment of abdomen capable of great distention and destitute of pubescence; last segment of body conspicuously narrowed. Spiracular disk (Plate LIV, 265) surrounded by four slender lobes, the ventral pair the longer, bearing at tip elongate hairs, some of which exceed the lobes in length; on lateral face at about midlength a small pencil of hairs; on ventral face one or two long setae; inner face of ventral lobes lined with pale brown, beginning as a narrow brown mark at tip, at about midlength gradually expanded into an elongate triangular mark, the two lines inclosing between their inner ends a pale linear mark; lateral lobes similar to ventral lobes, fringed with long yellow hairs which are longer than the lobes; inner face of lateral lobes lined with pale brown. Spiracles rather large, separated by a distance equal to about one and one-half diameter of one. Anal gills pale. A few setae in transverse alinement on last segment behind lateral lobes. Two pairs of short black setae behind gills.

Head capsule and mouth parts very similar to those of Hexatoma, dorsal plates of capsule separate from each other, not fused as in the Ulomorphae; inner margins of dorsal plates straight and parallel. Labral sclerite broadly transverse, narrowed at ends, lateral margins produced into long lobes which are densely tufted with short, golden-yellow hairs. Median lobe of epipharyngeal region projecting, provided with two large sensory papillae, one on either side, and a few other setiferous papillae near tip, surrounded by numerous hairs.

Antenna elongate, a little narrower at base, at tip with three or four hyaline, seta-like papillae which are of various diameters and shorter than the segment, the largest of these papillae delicately sculptured with transverse lines. Mandible acute, curved, at about midlength with a blunt, flattened tooth, this with a smaller similar tooth in its axil. Maxillary blade very long and slender, about half length of capsule.

Pupa.— Length: male, 13.2–15.2 mm.; female, 14–15.4 mm.
Width, d.-s.: male, 2.1–2.2 mm.; female, 1.8–1.9 mm.
Depth, d.-v.: male, 2.1–2.3 mm.; female, 2.2 mm.

Young pupae very pale; soft abdomen almost white; chitinized anterior part of body very pale brown. Older pupae much darker, the chitinized part becoming black with a bronzy reflection; abdomen very dark brownish gray; breathing horns dark brown on apical half.

Cephalic crest (Plate LV, 275) very prominent, elongate, tapering to the subacute tips; lobes with blunt tubercles behind, as well as four long setae on each lobe, three on dorsal margin and a longer one on lateral face at about midlength; viewed from in front, lobes separated by a broad, square or U-shaped notch; ventral part of crest produced forward between antennal bases as a depressed lobe bearing a stout seta on either side. Tubercle on antennal scape very prominent. A slightly smaller tubercle on either side of clypeus, with a small rounded knob cephalad of each. Labrum truncated. Labial lobes roughly diamond-shaped. Maxillary palpi very broad, rectangular, tips truncated. Antennal sheaths of male greatly elongated, enlarged at base; viewed from beneath, the swollen bases nearly contiguous on median line, just above and proximad of inner margin of eye, with scapal tubercle described above. Antenna of male exceeding wing pads, those of female ending just beyond wing base. Pronotal breathing horns short and stout, straight, transversely wrinkled, directed cephalad, dorsad, and laterad; when viewed from beneath, completely concealed by large cephalic crest. Thoracic notum convex; mesonotum transversely wrinkled (Plate LV, 277); median lobe of mesonotal scutellum projecting dorsad and caudad as a blunt point (Plate LV, 272). Two or three setae above wing axil. Lateral angles of thorax subacute, with a weak seta. Wing sheaths attaining end of second abdominal segment. Leg sheaths ending before caudal margin of third abdominal segment; tarsi of hind legs the longest, the two inner pairs ending about on a level (Plate LV, 273).

Abdominal segments (Plate LVI, 285) divided into a basal and a posterior ring; tergites on posterior ring with a subterminal transverse row of spines, these varying from about thirty-two on segment 3 to about fourteen on segment 7; these rows of spines interrupted on dorso-median line; at each end of row, three long setae, and two additional groups of setae interspersed along row; two setae on either side at anterior-lateral angle of ring; tergites on basal ring unarmed; sternites on posterior ring with a subterminal transverse row of from twenty-four to thirty-two spines, with two setae at each end of row; an isolated seta on caudo-lateral margin, close to pleura; a group of two approximated setae near base of posterior ring, on either side, about at level of spiracles. Sternites on basal ring unarmed; pleurites on basal ring with a solitary seta at about midlength, but slightly nearer dorsal margin; posterior ring with two setae dorso-caudad of spiracle, and a third seta ventrad of it. Male cauda (Plate LVI, 286) very blunt, much narrower than remainder of abdomen; ventral lobes very blunt; dorsal lobes short, stout, ending in sharp points directed dorsad, on outer face a long and a short seta; segment 8 with a dorsal trapezoid of four lobes, the posterior

pair the longer, each with two setae; anterior pair of lobes a little more widely separated; laterad of latter pair of lobes, a tubercle bearing three setae; a long, powerful seta on pleura; two setae on either side of median line of sternum. Female cauda (Plate LV, 274) similar, but ventral lobes more pointed, slightly exceeding level of dorsal lobes.

Nepionotype.— Ithaca, New York, April 18, 1917.
Neanotype.— Fall Creek, Ithaca, May 2, 1913.
Paratypes.— Several hundred larvae and pupae with types.

Eriocera fultonensis Alex.

1912 *Eriocera fultonensis* Alex. Psyche, vol. 19, p. 168–169, pl. 13, fig. 7.

Eriocera fultonensis is a rather common but usually local species thruout the northeastern United States. The larvae are found in the same situations as are described for the other species of the genus, in sand or gravel near the margins of usually large streams. On May 30, 1913, larvae were found in considerable numbers along the banks of Fall Creek, Ithaca, New York, where they occurred in company with numerous larvae and pupae of *E. spinosa*, a few large tabanid larvae, a small tabanid pupa, and the following beetle associates: Bembidion, Schizogenius, Tachys, Gastrolobium, and a few others. The pupal duration is seven days (from May 31 to June 6, 1913).

Larva.— Length, 18–26 mm.
Diameter, 2–2.3 mm.

Color, pale flesh yellow; anterior segments of body a little darker.

Body long and slender. Spiracular disk (Plate LIV, 266) with ventral lobes long and slender, lateral lobes shorter; ventral lobes at their tips with one or two very elongate blackish hairs which are from two to three times length of lobes; in addition to these the usual apical fringe of yellowish hairs not exceeding lobes; near base on outer side a small pencil of hairs; each ventral lobe with a very delicate capillary black line which expands abruptly at its inner end into a brown area, these two areas inclosing between their proximal ends a more or less oval pale area (in some specimens the inner ends completely encircling this pale area, while in others the brown lines are not continuous over the disk); lateral lobes shorter, similarly fringed with yellow hairs which are longer than lobes; inner face of lobes with a capillary black line. Spiracles rounded oval, widely separated.

Head capsule and mouth parts almost as in *Hexatoma megacera* and *Eriocera longicornis* as already described; epipharyngeal region (Plate LIV, 268) produced into a hemispherical rounded lobe which is densely covered with fine hairs; two large papillae on either side near tip, between them a terminal tuft of long yellow hairs surrounding two long, slender, setiferous papillae. Antenna with sensory papillae at tip short, about one-third length of segment.

Pupa.— Length, 14–16 mm.
Width, d.-s., 1.8–2 mm.
Depth, d.-v., 2.5–2.7 mm.

Fully colored pupae dark brown; cephalic crest paler; pronotal breathing horns pale yellow, darkening into brown at tips; wing pads light yellow, with dark venation showing clearly; pleurites of abdomen of a darker brown than sternites or tergites.

Body somewhat similar to that of *E. longicornis*, but general form much stouter. Cephalic crest (Plate LVI, 287) prominent, tuberculate, consisting of four lobes, the posterior lobes somewhat the larger, on posterior and lateral faces with two stout setae; a stout seta on ventral face of anterior lobes. Scapal spine lacking. Clypeal tubercles large, blunt, with a small setiferous tubercle above each. Labrum bluntly rounded at apex. Labial lobes elongate, diamond-shaped, tips rather acute. Pronotal breathing horns rather long and slender, transversely wrinkled, longer than cephalic crest. Mesonotum (Plate LV, 279) more convex than in *E. longicornis*. Wing pads usually showing venation clearly on pale background; vein *r* connecting R_1 with R_{2+3} distinctive of this species, lack of cell M_1 separating this pupa from that of *E. spinosa* and *E. brachycera*. Legs sheaths ending about on a level, the hind tarsi a little longer than the two inner pairs.

Arrangement of setae on abdomen (Plate LVI, 288) about as in *E. longicornis*. Pleura with two stout setae dorsad and caudad of each spiracle, and a weak seta ventrad of spiracle and close to it; basal ring with a single pleural seta; spicules on caudal margin of posterior ring small and numerous, on intermediate segments about forty in number; seventh sternite with about four to six spines at each end of row, the broad median area devoid of spines. Female cauda (Plate LV, 276) with tergal valves exceeding the long sternal valves, scarcely directed dorsad (this condition may be compared with that in *E. longicornis*). Male cauda with abdomen bluntly rounded at tip.

Nepionotype.— Ithaca, New York, May 30, 1913.
Neanotype.— With type larva, June 6, 1913.
Paratypes.— Larvae and pupae with types.

Genus **Penthoptera** Schiner (Gr. *sorrow + wing*)

1863 *Penthoptera* Schin. Wien. Ent. Monatschr., vol. 7, p. 220.

Larva.— Spiracular disk surrounded by four blunt lobes, the ventral pair a little the longer, inner face not marked with darker, at tip with one or more long setae. Head capsule about as in Eriocera. Coloration a deep saturated yellow.

Pupa.— Cephalic crest with lobes rounded, setiferous. No distinct tubercles or spines on head or thorax. Pronotal breathing horns short, stout, cylindrical, apex expanded into a flattened head, stem coarsely wrinkled, base enlarged. Abdominal armature weak. Spiracles not well developed.

Penthoptera is a small genus which includes four European and three American species, two of the latter occurring in tropical America. The eastern North American *Penthoptera albitarsis*, discussed below, has been considered in some detail by the author in another paper (Alexander, 1915c: 152–157).

Penthoptera albitarsis O. S.

1869 *Penthoptera albitarsis* O. S. Mon. Dipt. N. Amer., part 4, p. 257–258.

The larvae of *Penthoptera albitarsis* are usually not uncommon in rich organic mud in shaded places thruout the range of the species. Larvae of many sizes, some very small, others apparently almost fully grown, may be found at a single time. This would probably indicate that the species emerges at intervals thruout the summer, rather than that it is double-brooded.

Larva.— Length, 10–12 mm.
Diameter, 1–1.2 mm.

Color bright chestnut-yellow, anterior half of body richer- and deeper-colored; thoracic segments suffused with brown; skin with a silky, iridescent reflection.

Body provided with numerous long, appressed hairs. A few setae on body, the following being the most conspicuous: one on lateral dorsal margin of last segment, near base of lateral lobes; a series of four groups of one or two in each row across dorsal surface of the three thoracic segments at about midlength; a group of two or three long setae on sides near caudal margin of segments. Subterminal enlargement of abdomen with about twenty-five transverse rows of fine points.

Spiracular disk (Plate LVII, 292 and 293) with four blunt lobes; ventral lobes densely fringed with long, pale hairs, those toward ends of lobes longer; one or more elongate setae near tip of each ventral lobe, these being longer than lobes themselves; lateral lobes with a similar fringe of rather short, yellow hairs; spiracular disk almost free from dark markings, a pale brown line extending dorsad from each spiracle and an indistinct brownish line along ventral margin of lateral lobes. Spiracles circular. Anal gills four, pale. Head capsule rather broad, dorsal plate with inner anterior angles rounded. Labrum (Plate LVII, 289) almost as in *Eriocera spinosa*, the extreme cephalic epipharyngeal parts with the usual papillae and setiferous tubercles; lateral papillae bearing at their tips three or four slender pegs; between these papillae two pairs of setiferous tubercles, a basal larger pair and a more apical smaller pair. Mandible (Plate LVII, 291) a little more curved than is usual in this subtribe, inner margin with a double tooth at about midlength.

Pupa.— Length, 10–10.5 mm.
Width, d.-s., 1.4–1.5 mm.
Depth, d.-v., 1.5–1.6 mm.

Thorax dark brown, wing and leg sheaths paler; pronotal breathing horns dark brown, swollen bases and tips much paler, light orange; abdomen brownish yellow.

Cephalic crest consisting of two widely separated rounded lobes behind, each bearing two setae; anteriorly the crest appearing as a large depressed lobe between antennal bases, with a very large, stiff seta on either side. A powerful seta on each side of region of clypeus. A seta on genal region between eye and sheath of maxillary palpus. Labrum evenly rounded or a little truncated at apex. Labial lobes widely separated, roughly rounded or indistinctly pentagonal in outline. Maxillary palpi broad, ending bluntly beneath or just before antennal sheaths. Antennae ending just beyond wing root in female, considerably longer in male

Pronotal breathing horns (Plate LVII, 294) short, stout, cylindrical, apex expanded into a flattened circular head, stem coarsely and transversely wrinkled, base enlarged; breathing horns widely separated at their bases, but bent proximad so as to be almost contiguous at their tips; two strong setae laterad of base of breathing horn and an additional one in front of it. Mesonotum transversely wrinkled, with a distinct carina anteriorly (Plate LVIII, 296). Two groups of two setae on either side of median line, with an additional solitary seta; two longer setae above wing axil. Wing sheaths ending before tip of second abdominal segment. Leg sheaths ending at from two-thirds length to opposite end of third abdominal segment; tarsal sheaths ending about on a level, or, in some specimens, the hind tarsi a little longer than the others (Plate LVIII, 297).

Abdomen indistinctly divided into a narrow basal ring and a broader posterior ring; basal ring further very indistinctly subdivided into two subequal annuli. Abdominal armature weak; on sternites a subterminal transverse row of delicate spines with two setiferous tubercles at each end of row; on posterior ring two setae on either side at about midlength; tergites with four groups of two or three setae near posterior margin and an additional group of two setae on lateral margin of posterior ring near base; pleural region with a stiff seta on extreme anterior part of basal ring. Spiracles distinct; a group of two setae caudad and slightly ventrad of each spiracle, with an additional solitary seta caudo-ventrad of these. Female cauda (Plate LVIII, 298) with tergal valves of ovipositor only a little longer than sternal valves, at tip ending in a short, rather blunt point directed dorsad; on outer face before tip a short, stiff seta; segment 8 on dorsum with a close trapezoid of four irregular lobes; two setiferous tubercles on dorsal and lateral part of eighth segment, the more dorsal of these with two setae, the lateral one with a single seta; sternum with four stout setae, of which two are lateral and two are median in position. Male cauda (Plate LVII, 295, and Plate LVIII, 299) with sternal valves short and blunt; tergal valves slender, ending in an acute point directed dorsad; a few short setae on outer face before tip.

Nepionotype.— Ithaca, New York, May 25, 1917.
Neanotype.— Bool's hillside, Ithaca, June 5, 1917.
Paratypes.— Abundant larvae and a few pupae with types.

Subtribe **Polymeraria**

Genus **Polymera** Wiedemann (Gr. *many* + *part*)

1821 *Polymera* Wied. Dipt. Exot., vol. 1, p. 40.

Polymera is a tropical American genus including fifteen described species, one of which, *Polymera georgiae* Alex., occurs in the southeastern United States. A single additional species, *P. magnifica* Meunier (1906: 385), has been described from the Baltic amber (Lower Oligocene). The only species concerning the ecology of which we have any record is *P. geniculata* Alex., which has been found living in crabholes beneath rocks in Porto Rico. In this connection the long-horned deinoceritine mosquitoes

which live in similar habitats should be considered. Howard, Dyar, and Knab (1915: 213) say, in describing these mosquitoes:

> These crab-hole inhabiting species possess peculiarly developed antennae in order, as we suppose, to enable them to detect the approach of their crustacean host and fly out of the holes before being overwhelmed in the water in the bottom by the incursion of the crab, whose body must completely fill the entrance to the hole.

It is curious and suggestive that the males of Polymera should likewise possess elongated and very complicated antennae.

Tribe Pediciini

The Pediciini constitutes a small tribe which seems to be divisible into two well-marked subtribes, the more generalized Adelphomyaria indicating a relationship with the Hexatomini.

The larvae of the Pediciini have the labrum broad and the epipharynx usually feebly armed. The mentum is completely divided into two parts, each half with not more than four, usually three, teeth. The hypopharynx is labriform. The maxilla consists of two lobes, distinct and separate in the Adelphomyaria, more or less approximated or fused in the Pedicaria. The mandible is powerful, ending in a strong apical point; the cutting edge has about four teeth; there is a simple tuft of setae on the prosthecal region in the Dicranotae and in Pedicia. The head capsule is very elongate, massive, and compact, with the posterior incisions very shallow. In the Adelphomyaria the cauda is surrounded by four lobes which are fringed with exceedingly elongate hairs; in the Pedicaria there are two ventral caudal lobes, each tipped with a very few setae. The anal gills are four in number and are segmented, the terminal segment being more or less retractile. In the Pedicaria prolegs are developed on the abdominal segments of some of the genera.

All of the species of the tribe, so far as is known to the writer, are carnivorous in their larval state, which is spent in mud or earth close to water.

The two subtribes of the Pediciini may be separated as follows:

Larvae

Spiracular lobes four in number, fringed with very long, delicate hairs. *Adelphomyaria* (p. 895)

Spiracular lobes two in number, ventral in position, each tipped with from six to eight setae. *Pedicaria* (p. 899)

The most important literature on the tribe Pediciini is as follows:

Pedicia rivosa	General	Scheffer, in Rossi, 1848:9.
Pedicia rivosa	Larva, pupa, general	Beling, 1879:45–46.
Pedicia rivosa	General	Reuter, 1893.
Pedicia rivosa	General	Wesenberg-Lund, 1915:335.
Pedicia albivitta	Larva	Needham, 1903:285–286; 1905:8.
Tricyphona immaculata	Larva, general	Beling, 1879:47.
Tricyphona immaculata	Larva, pupa, general	De Meijere, 1916:195–196.
Tricyphona schineri	Larva, pupa, general	Beling, 1879:47.
Dicranota bimaculata	Larva, pupa, general	Miall, 1893.
Dicranota bimaculata	Larva, pupa	Grünberg, 1910:66–67. (Copy.)
Dicranota bimaculata	General	Wesenberg-Lund, 1915:342–343.
Dicranota bimaculata	Larva	Malloch, 1915–17 b:219–220. (Copy.)
Rhaphidolabis tenuipes	Larva, general	Needham, 1908 a:212–214.

Subtribe **Adelphomyaria**

The division Adelphomyaria, as known, includes but the single genus Adelphomyia Bergroth, a curious genus of small crane-flies which, in the general appearance of the adults, strongly suggest the hexatomine subtribe Limnophilaria. The immature stages have not been associated with the adult flies by rearing, and there is, of course, the possibility of a mistaken reference. The immature stages of the insect herein described are easily recognized, however, and, no matter to what group it belongs, it deserves subtribal rank under the Pediciini.

Genus **Adelphomyia** Bergroth (Gr. *brother* + *fly*)

1891 *Adelphomyia* Bergr. Mittheil. Naturf. Ges. Bern, 1890, p. 134.

Larva (supposition).— Body with pencils of stiff setae, producing a spiny appearance. Spiracular disk surrounded by four short lobes which are fringed with exceedingly elongate hairs. Spiracles large, separated by a distance less than the diameter of one. Head capsule long and massive, all the plates firmly united except behind. Mandible acutely pointed. Maxilla of two elongate separated lobes. Antenna two-segmented, the terminal segment with three small papillae. Hypopharynx labriform. Mentum completely divided, each half with four teeth, the middle pair on each side the largest (*minuta*, supposition) or the second from the inside the largest (*americana*, supposition).

Pupa (supposition).— Cephalic crest small, each lobe with three setiferous tubercles. Pronotal breathing horns moderate in length, broadly tipped with light yellow. Mesonotum unarmed. Wing sheaths extending beyond base of third abdominal segment. Leg sheaths extending to beyond base of fifth abdominal segment. Abdominal armature weak, especially on posterior segments.

Adelphomyia is a small genus of crane-flies, including but four European and three North American species, and a doubtful species from Africa. The

insects resemble tiny species of the genus Limnophila. The adult flies are not uncommon on rank herbage, especially ferns, in woods and usually near running water. As already stated, the immature stages have not been reared, but larvae found by the writer in Maine are referred with considerable confidence to *Adelphomyia americana* and *A. cayuga*, while larvae and pupae of another species taken at Ithaca, New York, seem to be those of *A. minuta*. The larvae show a curious combination of tribal characters. The general appearance and the structure of the spiracular disk are altogether those of one of the Hexatomini; but the head capsule and the details of the mouth parts indicate a relationship with the Pediciini that cannot be denied.

Adelphomyia minuta Alex. (supposition)

1911 *Adelphomyia minuta* Alex. Can. Ent., vol. 43, p. 287–288.

Adelphomyia minuta is a characteristic late spring species, common in boggy woods and on vegetation along rapid streams. Larvae and pupae which are referred to this species were sifted from organic mud taken on Bool's hillside, Ithaca, New York, thruout May and early June, 1917. The pupae referred to this species strongly resemble those of Dicranophragma but in reality are very different. The species is discussed herewith in the hope that it may be definitely recognized in the future.

Larva.— Length, 4.5–5 mm.; caudal fringe, 2 mm. additional.
Diameter, 0.4 mm.

Coloration, saturated yellow with a faint orange-brown tinge.

Form narrow, body tapering gradually to both ends, spiracular disk narrowed. Body clothed with a delicate appressed pubescence and numerous tufts of conspicuous stiff hairs which produce a spiny or bristly appearance; the more conspicuous of these tufts located on pleural region, there being three such rows on abdominal segments — one on basal ring, the second and largest at base of posterior ring, and the third just before posterior margin of segment and more ventral in position; only the large intermediate tuft present on thoracic segments, the small brush on anterior annulus of abdominal segments lacking. Spiracular disk (Plate LIX, 305) with four lobes; ventral pair not more than three times length of lateral pair; inner face of lobes margined with brown; at tip of ventral lobes a fringe of exceedingly elongate hairs, which are from one-third to nearly one-half length of entire body and about fifteen times length of lobes bearing them; a stiff sensory bristle located in black margin at tip of lobe; lateral lobes with fringe of hairs relatively much shorter, tho still long. Spiracles large, close together, separated by a distance less than diameter of one, the middle piece black, the ring pale yellow. Anal gills four, slender, hyaline, each subdivided by constrictions into four lobes which are gradually narrowed from the base outward, the last being cylindrical.

Head capsule very compact, lateral plates united with broad dorsal plate except for a short distance behind. Labrum (Plate LIX, 300) broadly transverse; cephalic margin truncate or very slightly concave; epipharyngeal region with about five transverse interrupted rows of setae. Mentum (Plate LIX, 302) of two entirely separated plates, each half with four teeth, those at the ends the smallest, the outermost tooth tending to be reduced, the two middle teeth of each side notably larger than the others; outside of mentum a thin plate, its inner proximal margins nearly contiguous at median line of body. Hypopharynx labriform, projecting beyond level of both labrum and mentum; outer lateral angles densely hairy, median posterior area with about eight small, hyaline spines. Antenna (Plate LIX, 301), in caustic-potash mounts, hyaline; basal segment elongate-cylindrical, bearing at its tip about two papillae as follows: a long, slightly curved, cylindrical papilla which is finely sculptured, and immediately proximad of this a slightly smaller second segment of the antenna, bearing near its tip three tiny papillae, an inner flattened subspatulate blade, and two longer cylindrical papillae; near base of this second antennal segment a long seta. Mandible (Plate LIX, 303) rather long and slender, apical point narrow; about four small lateral teeth near ventral cutting edge, the most basad of these acute; a large dorsal tooth on cutting edge and two very small acute teeth near base; on dorsal face of mandible two long setae, and two somewhat shorter setae near heel of mandible; about five or six stout setae at prosthecal region. Maxilla (Plate LIX, 304) consisting of two elongated lobes which are separate from each other, the outermost the longer, the pale rounded palpus terminal in position; inner lobe shorter, with three elongate setae, of which one is apical and the longest is sub-basal in position.

Pupa.— Length, 4.5–4.7 mm.
Depth, d.-v., 0.8 mm.

Color light yellowish brown, the thoracic dorsum paler; pronotal breathing horns dark brown, apical quarter abruptly light yellow; abdomen brown, lateral and posterior parts of each segment darker.

Cephalic crest small, each lobe with three small setiferous punctures on anterior face; ventrad of crest between antennal bases a prominent median lobe. Labrum broad; apex truncated, indistinctly bifid. Labial lobes large, with a deep U-shaped median notch behind. Maxillary palpi rather short and stout, ending before joint of fore legs (Plate LX, 307). Pronotal breathing horns moderately elongate, curved slightly laterad, strongly divergent, cylindrical, of uniform diameter thruout their length. Mesonotum not very gibbous (Plate LX, 306). Thorax with a high anterior median carina. Wing sheaths extending beyond base of third abdominal segment, the venation indistinct. Leg sheaths rather long, ending at about one-third length of fifth abdominal segment; hind legs much longer than the others, middle legs a very little longer than fore legs.

Abdominal segments indistinctly subdivided into two rings, a narrow anterior ring and a much broader posterior ring; abdominal armature very weak, lacking on segment 7; basal annulus on tergites and sternites with a number of small pits on sides, these sometimes sparse or lacking; posterior ring with a transverse row of numerous long, stout setae or delicate spines before margin. Spiracles weak, at base of posterior ring. Male cauda (Plate LX, 309 and 310) with sternal lobes elongate, contiguous except at extreme tips; tergal lobes terminating in very slender and acute curved points, directed caudad and dorsad; tergite

8 swollen, with four blunt lobes, the posterior pair large, with their posterior faces setiferous. Female cauda (Plate LX, 308) with sternal valves much shorter than tergal valves and rather blunt at tips; tergal valves broad at base, narrowed at tips, which terminate in acute black spines, situated on lateral margin before apex, the spines directed dorsad, laterad, and caudad.

The larvae were common near Ithaca, New York, from May 10 to June 5, 1917. The pupae are described from one male and two females washed from mud from Bool's hillside, at Ithaca, on June 11, 1917. A little later in June adult flies of this species were common at this location.

Adelphomyia americana Alex. (supposition)

1912 *Adelphomyia americana* Alex. Pomona Journ. Ent., vol. 4, p. 829–831.

Larvae that were rather common in the rich organic mud from the Standpipe Woods, Orono, Maine, from July 1 to 14, 1913, are referred with some doubt to *Adelphomyia americana*. They are unquestionably congeneric with the species last described (*A. minuta*, supposition) and with the form discussed in the following pages as *A. cayuga*. A short time after the larvae of these three species were obtained, the adult flies appeared in considerable numbers in the same situations and there seems to be but little doubt as to the reference. Associated with the larvae of this species in the organic mud were a few larvae of Penthoptera, Rhaphidolabis, and other species of crane-flies.

The larva of the present species averages larger than that of *A. minuta*, when fully grown measuring 5.5 millimeters in length. In coloration it is light yellow. The ventral lobes of the spiracular disk have the dark markings on their inner face much more extensive, the apical half being suffused with brown. The mouth parts are similar to those of *A. minuta* as described, but the outermost of the two large teeth of each half of the mentum is reduced in size so that only a single tooth is of conspicuous size.

(Described from larvae taken at Orono, Maine. No. 66–1913.)

Adelphomyia cayuga Alex. (supposition)

1912 *Adelphomyia cayuga* Alex. Pomona Journ. Ent., vol. 4, p. 831.

The supposed larva of *Adelphomyia cayuga* occurred with specimens of the preceding (*A. americana*, supposition) at Orono, Maine, from July 1 to 13, 1913. This is a smaller species than the preceding, measuring but 4 millimeters in length, and is much paler, the color being almost

white. The condition of the mental teeth is almost as in *A. americana*, but the outermost of the two large intermediate teeth is a little larger. The larvae were rather frequent in the mud beneath saturated moss.

(Described from larvae taken at Orono, Maine. Nos. 57– and 67–1913.)

Subtribe **Pedicaria**

The Pedicaria comprise a well-defined division of the tribe Pediciini, including two groups of genera — the more generalized Pediciae, with the genera Pedicia, Tricyphona, Ornithodes, and Rhaphidolabina, and the specialized Dicranotae, with the genera Dicranota, Rhaphidolabis, and probably Polyangaeus.

The genera of the Pedicaria may be divided in the main as follows:

Larvae

1. Abdomen without prolegs, but with raised welts on segments 4 to 7, these covered with a microscopic scurfiness. (Group *Pediciae*) 2
   Abdomen with conspicuous cylindrical prolegs on segments 3 to 7, these with circlets of conspicuous chitinized hooklets around their ends . . . . Group *Dicranotae* (p. 906)
2. Abdominal segments 4 to 7 with raised welts on both dorsal and ventral surfaces; sides of hypopharynx not parallel, narrowed toward base . . . . *Rhaphidolabina* Alex. (p. 901)
   Abdominal segments 4 to 7 with welts on ventral surface only; sides of hypopharynx subparallel 3
3. Size very large, when fully grown 40 mm. in length; mental plates without a small lateral tooth . . . . *Pedicia* Latr. (p. 899)
   Size smaller, when fully grown under 30 mm. in length; mental plates with a small lateral tooth . . . . *Tricyphona* Zett. (p. 903)

The writer is unable to separate the genera of the group Dicranotae with the material available, and is inclined to suspect the congenerousness of Rhaphidolabis with Dicranota. The characters given by Malloch (1915–17 b: 217) to separate the two genera do not hold at all in a series.

It is impossible also to key the pupae with the present knowledge of the group.

Group **Pediciae**

Genus **Pedicia** Latreille (Gr. *a field*)

1809 *Pedicia* Latr. Hist. Nat. Crust. et Ins., vol. 4, p. 255.
1916 *Daimiotipula* Matsumura. Thous. Ins. Japan, add. 2, p. 463.

Pedicia is a small genus including but six described species, one occurring in Europe, one in Japan, and four in North America. Of the last-named,

two are eastern and two are western in their distribution. They include the largest and most beautiful species of the Limnobiinae.

The European *Pedicia rivosa* (Linn.) was found by Beling (1879:45–46) living in brooks and springs, or in wet spots among saturated leaves and other débris, sometimes associated with the larvae of *Tipula lutescens* Fabr. The pupae live in cylindrical vertical burrows, clothed in the last larval skin, and are able to move up and down in these passages Pupation lasts from one to two weeks.

Needham (1903:285–286, and 1905:8) was the first to describe and figure the larva of the commonest eastern species, *Pedicia albivitta* Walk.

Pedicia albivitta Walk.

1848 *Pedicia albivitta* Walk. List Dipt. Brit. Mus., vol. 1, p. 37.

Pedicia albivitta is a beautiful fly, common and widely distributed thruout the northeastern United States and Canada. The adults are on the wing in midsummer, and a few individuals may usually be found in June. The much rarer and more local *P. contermina* Walk. is a vernal species, on the wing in May and early June.

The larvae of *P. albivitta* live in cold springs and beneath saturated moss at the edge of streams. The writer has never succeeded in rearing this species to the adult condition.

Larva.— Length, 40–44 mm.
Diameter, 5–5.5 mm.

Color dark grayish brown above, paler at sutures and on posterior half of body; paler beneath, more grayish.

Body covered with a short, appressed, dusky pubescence. Thoracic segments with a pencil of small setae on pleural region. Abdominal segments with a few delicate lateral setae on posterior ring, at about midlength of segments. Ventral creeping-welts on abdominal segments 4 to 7 completely divided on median line, the welts covered with a microscopic scurfiness. Spiracles (Plate LXI, 311) circular, separated by a distance about equal to diameter of one, situated on a slightly protuberant elevation. Spiracular lobes two, ventral in position, short, slender, each with about six setae at tip. Anal gills (Plate LXI, 315) short, stout at base, before tip a constriction cutting off the elongate conical terminal segment, which is partly telescopic within the next basal segment.

Head capsule (Plate LXI, 312) massive, elongate, as in this division. Labrum broadly transverse, lateral parts a little enlarged and projecting anteriorly into blunt lobes, with a long seta near inner margin; median region of labrum with two widely separated setae, just laterad of each of which is a small papilla. Epipharynx roughened into a narrow transverse band of small spines. Mentum completely divided, each half continuous with ventral plate

of same side; anterior margin of each half with three slender, flattened teeth, the middle one of which is slightly the shortest. Hypopharynx conspicuous, labriform; anterior margin with a deep notch to form distinct lobes at lateral angles, and with several rows of small chitinized tubercles. Antenna (Plate LXI, 313) small; basal segment elongated, slightly curved, a circular auditory plate near base, at tip with numerous papillae, two of which are very long, nearly as long as segment itself; in addition to these, three or four tiny cylindrical papillae. Mandible powerful; ventral cutting edge with a row of about four teeth which are successively enlarged from tip to base; basal tooth very broad and flat, with outer margin truncate or slightly concave; teeth on dorsal cutting edge indistinct; a pencil of moderately delicate setae on scrobal region of mandible, and another at prosthecal region. Maxilla elongate; outer lobe larger than inner lobe, chitinized, apex with a very flat circular palpus (Plate LXI, 314) which is provided with a few disklike papillae around margin and a few scattered sensory papillae over pale apex; inner lobe with a long, powerful seta on ventral face and smaller setae near tip.

Nepionotype.— Ithaca, New York, June 1, 1917.
Paratypes.— Larvae from type locality.

Genus **Rhaphidolabina** Alexander (Gr. diminutive of *Rhaphidolabis*)

1916 *Rhaphidolabina* Alex. Proc. Acad. Nat. Sci. Phila., p. 540–541.

Larva.— Body covered with an abundant, appressed pubescence and tufts of erect hairs which are more numerous on anterior end of body. Creeping-welts on dorsal and ventral surfaces of abdominal segments 4 to 7. Spiracular lobes two, moderately elongated, each with about six hairs at tip. Spiracles large. Anal gills four, long and diaphanous. Head capsule long and massive. Mandible powerful. Antenna short, with two elongate papillae. Hypopharynx labriform, anterior margin concave. Mentum completely divided, each half with three large teeth and a much smaller lateral tooth.

Pupa.— Labrum truncate. Pronotal breathing horns short-cylindrical or slightly flattened. Abdominal segments with circular areas of spicules on pleurites. Intermediate tergites with a broad transverse band of tiny spines.

The genus Rhaphidolabina includes only *R. flaveola*, a curious pallid fly of the northeastern United States, serving as a connecting link between Tricyphona on the one hand and the Dicranotae on the other. The adult flies are common on rank vegetation in cold woods. The immature stages are spent in rich organic earth in the same situations as are frequented by the adult flies.

Rhaphidolabina flaveola (O. S.)

1869 *Rhaphidolabis flaveola* O. S. Mon. Dipt. N. Amer., part 4, p. 288.

The writer has found the larvae of *Rhaphidolabina flaveola* in Maine and in New York. At Orono, Maine, larvae were numerous in the rich

organic mud of the Standpipe Woods. One large larva was placed in a watch crystal with a fully grown larva of *Adelphomyia cayuga* (supposition). It at once seized the latter in its mandibles at about the third abdominal segment, and carried it helplessly all around the dish, occasionally shaking it, quite as a terrier does a rat.

Larva.— Length, 9.8 mm.
Diameter, 0.8 mm.

Color, brown to orange-yellow on anterior segments of body, becoming darker on abdominal segments due to the increase of pubescence.

Body covered with an abundant, appressed pubescence. Form terete; body moderately elongated, gradually narrowed toward both ends. Abdominal segments 2 to 8 divided into a narrow basal ring and a much broader posterior ring; segments 4 to 7 with conspicuous dorsal and ventral welts, which are larger and more conspicuous on posterior segments; these welts occupying basal ring of segments, and bisected by a deep longitudinal median impression, their surface covered with microscopic points. Thoracic segments before mid-length with a transverse row of stiff, dark brown hairs grouped in tufts or pencils; these hairs occurring on abdominal segments also, but less prominent here and occupying posterior region of segments; pencils more numerous on ventral and pleural regions, much scantier on dorsal surface except on pronotum. On sides of last abdominal segment, between spiracles and spiracular lobes, several long setae arranged in a transverse row, lacking on mid-dorsal and ventral regions. Spiracular disk (Plate LXII, 321) reduced to two ventral lobes, as in this division, these lobes slightly united basally, not very elongate, blunt at their tips, which bear about six dark setae. The two spiracles large and conspicuous, entirely exposed on dorsum of last segment, separated by a distance a little less than diameter of one; middle piece of spiracles large, black; ring brownish yellow. Anal gills four, long and slender, nearly hyaline, divided into lobes by slight constrictions; posterior pair of lobes a little longer than anterior pair.

Head capsule elongate, flattened, massive, as in this tribe. Labrum conspicuous, exceeding mentum and hypopharynx, the anterior margin fringed with long hairs. Mentum (Plate LXII, 316) completely divided, each half with three subequal prominent teeth and an additional much smaller lateral tooth; middle tooth of each side a little broader. Hypopharynx (Plate LXII, 317) labriform, anterior margin deeply concave, roughened. Antenna (Plate LXII, 318) short, the segment short-cylindrical, a little enlarged toward truncated apex; at tip several papillae, of which two are exceedingly elongate, very slender, about twice length of basal segment. Mandible (Plate LXII, 319) powerful, ending in an acute point; ventral cutting edge with about four teeth, the basal one of which is the largest, subtruncate, the next outer tooth a large, flattened, acute blade, two or three smaller flattened teeth just before tip; dorsal cutting edge with about two small teeth. Maxilla (Plate LXII, 320) short and very stout, the outer lobe much longer than the slightly smaller inner lobe.

Pupa.— (The following notes are taken from the cast pupal skins of the bred specimens

Labrum truncate. Labial lobes ovate. Maxillary palpi short and stout, broadest just beyond base, tips blunt (Plate LXII, 322). Antenna moderate in length, tapering gradually to tip. Pronotal breathing horn (Plate LXII, 323 and 324) short, cylindrical or

slightly flattened, with a row of circular breathing pores along margin of distal end, which is slightly enlarged. Wing sheaths short. Leg sheaths much longer.

Pleural region of abdominal segments with circular areas which are armed with abundant, short, straight or slightly arcuated, rows of spicules, there being from five to seven spicules in each row; under high magnification these appearing as flattened, scalelike tubercles, fringed with the spicules described above; dorsum of intermediate abdominal segments with a broad transverse band which is rather densely set with tiny, sharply curved spines; on posterior segments these rows lacking or much weaker; dorsal bands lying posterior to level of lateral areas. Male cauda (Plate LXII, 325) with dorsal plate rather small, each half indistinctly bilobed at tip; outer lobe minutely tuberculate and with a small seta; ventral lobes large, blunt at tips; eighth tergite on either side with a small tubercle bearing two setae.

Nepionotype.— Ithaca, New York, May 14, 1917.
Neanotype.— Ithaca, May 26, 1917. Cast pupal skin; larva placed in rearing May 14, 1917, emerged May 26, male.
Paratypes.— Larvae, with type larva. Pupae, taken as larvae May 27, 1917, placed in rearing, emerged June 7, 1917. No. 79 - 1917.

Genus **Tricyphona** Zetterstedt (Gr. *three + bend*)

1837 *Tricyphona* Zett. Isis von Oken, p. 65.
1856 *Amalopis* Hal. Ins. Brit., Dipt., vol. 3, p. 15.
1856 *Bophrosia* Rond. Dipt. Ital. Prodr., vol. 1, p. 183.
1860 *Crunobia* Kol. Wien. Ent. Monatschr., vol. 4, p. 391.
1881 *Nasiterna* Wall. Ent. Tidskr., vol. 2, p. 179, 191.

Larva.— Body moderately elongate, with ventral transverse creeping-welts on basal annuli of abdominal segments 4 to 7. Spiracular lobes two, moderately elongate. Anal gills four, divided into two to four lobes by from one to three constrictions. Head capsule massive, elongate. Eyespots distinct. Mandible powerful, ending in an acute point and with about four lateral teeth. Maxilla stout, consisting of two distinct lobes, the slender inner lobe closely approximated to the larger outer lobe. Antenna small; basal segment cylindrical at tip, with two exceedingly long, hyaline papillae (possibly lacking in *T. immaculata*). Hypopharynx labriform, anterior margin concave, roughened. Mentum completely divided, anterior margin of each half with three large teeth.

Pupa.— Pronotal breathing horns short and stout, blunt, angles rounded. Abdominal segments with transverse bands of spicules on tergites and sternites, and circular areas on pleurites.

Tricyphona is the largest genus of the Pediciini, including more than fifty described species. Almost all of these species are found in the Holarctic region, but two or three are Antipodal. In the eastern United States, *Tricyphona inconstans* is the most widely distributed and apparently the commonest species. This species and certain others (as *T. paludicola* Alex.) are characteristic swamp inhabitants, but other species

occur along running streams (*T. vernalis* [O. S.]) or near cliffs (*T. auripennis* [O. S.]).

The immature stages of the known species are usually spent in moist earth. In Europe, *T. immaculata* (Meig.) was reared by Beling (1879:47) from larvae taken beneath decaying vegetable mold in the bed of a dried-up woodland stream. Other specimens were found in old horse manure in beech woods. De Meijere (1916:195–196) found the same species in decaying leaves and other vegetable matter in wet spots near the banks of streams. *T. schineri* (Kol.) was found on August 19 in a wet spot in beech woods, where the larvae were associated with pupae of *Pedicia rivosa* in damp earth beneath débris, adults emerging on September 6 and 12 (Beling, 1879:47). The only American species whose immature stages have been found is *T. inconstans*, described herein.

Tricyphona immaculata (Meig.), the genotype, as described by De Meijere in the paper cited above, differs from *T. inconstans* as herein described in the following points: The antenna bears a very short terminal papilla instead of the two very long ones in the local species. The small lateral tooth on the mentum is not mentioned nor figured as appearing in *T. immaculata*. The anal gills are short and with but a single constriction. The pupa has the pronotal breathing horns small, kidney-shaped, the outer margin rounded. The fore legs are a little shorter than the middle legs, and these in turn are somewhat shorter than the posterior legs. The skin of the abdomen is very delicate, with crossrows of very small spicules, arranged in numerous irregular transverse rows, at the posterior margins of the segments, about seven such crossrows being present.

Tricyphona inconstans (O. S.)

1859 *Amalopis inconstans* O. S. Proc. Acad. Nat. Sci. Phila., p. 247.

Tricyphona inconstans is an abundant species thruout eastern North America. It has been recorded also from Europe, but the latter records are almost certainly erroneous. The writer found larvae of this species in rich mud at Larch Meadows, near Ithaca, New York, on May 15, 1917, in association with larvae of *Rhamphidia mainensis*, *Pseudolimnophila luteipennis*, and *P. inornata*. Adults emerged on May 27, 1917 (No. 52–1917). An account of the association in which these larvae occurred

is given in connection with the discussion of *Rhamphidia mainensis* (page 831).

Larva.— Length, 17–17.5 mm.
Diameter, 1.3 mm.

Color pale yellowish white; anterior parts of body sometimes a more saturated yellow. Form moderately stout, body a little narrowed toward ends; surface of body almost glabrous, the vestiture being a microscopic pale pubescence and scanty scattered hairs. Ventral surface of abdominal segments 4 to 7 with a prominent transverse welt, which is hollowed out medially so as to appear as paired prolegs, these being unarmed with hooks or points. Spiracular lobes short, divergent, tapering gradually to the blunt tips, which are provided with seven or eight setae. Spiracles (Plate LXIII, 330) on a transverse oval elevation, small, rounded, separated by a distance greater than diameter of one; middle piece of spiracles large, black, rings narrow. Anal gills four, very long and slender, constricted into about four lobes which are successively narrowed from the base outward, the terminal division very slender.

Head capsule of the usual elongate, massive type of this tribe. Labrum large, projecting beyond hypopharynx, anterior margin with long hairs. Mentum (Plate LXIII, 326) large, completely divided, each half with three subequal narrow teeth and an additional reduced lateral tooth; on proximal margin of each half of mentum, near base of innermost tooth, a few tiny notches dovetailing into those of opposite half. Hypopharynx (Plate LXIII, 327) projecting far beyond mentum, labriform; anterior margin deeply concave and provided with small rounded papillae; lateral angles smooth, rounded, subchitinized. Antenna (Plate LXIII, 328) small; basal segment cylindrical, bearing at its tip two elongate papillae which are about one-half longer than basal segment alone; besides these an oval papilla. Mandible (Plate LXIII, 329) of the usual pediciine type, powerful, the apex running out in a long, curved point; ventral cutting edge very flat, cut into about five teeth, the two basal of which are very large; the most basal of these teeth squarely truncated, the left mandible with an additional small tooth on lower inner angle of this blade; the next outer tooth rather acute; outermost teeth small and flattened; dorsal cutting edge, as usual with this division, with two very small teeth located far out on apical point; a tuft of a few long setae on back of mandible near heel. Maxilla (Plate LXIII, 329) powerful, as in this group of genera, but not exserted from the prothoracic orifice when head is retracted; outer lobe very stout, feebly chitinized basally, hyaline at apex, which bears the flattened, disklike palpus; inner lobe slenderer, shorter, with a few setae and small papillae.

Pupa.— (The following notes are taken from the cast skins of the reared specimens.)

Labrum with apex broadly triangular. Labial lobes large, ovate, tips narrowed and bluntly rounded (Plate LXIII, 331). Pronotal breathing horns (Plate LXIII, 332 and 333) very short, stout, roughly cylindrical, the apices truncated; in lateral outline, pentagonal, with a row of breathing pores around margin of truncate apex. Thoracic dorsum transversely roughened by short, irregular grooves.

Abdominal sternites with broad transverse bands of spicules on segments 5 to 7, the last of these three bands the weakest; similar bands on tergites 4 and 5, these bands subequal in size; pleural region with a large, roughly circular area of short rows of microscopic spicules,

these areas near base of segments. Female cauda (Plate LXIII, 334) with tergal valves elongate, tapering gradually to the rather blunt tips; sternal valves very small, blunt at tips; at base, on dorsal side of eighth segment, two setiferous tubercles.

Nepionotype.— Larch Meadows, Ithaca, New York, May 15, 1917. No. 52-1917.
Neanotype.— Ithaca, May 27, 1917, a cast pupal skin.

Group **Dicranotae**

Genus **Dicranota** Zetterstedt (Gr. *a fork*)

1838 *Dicranota* Zett. Ins. Lapponica, Dipt., p. 851, no. 164.

Dicranota is a small genus of crane-flies (about fifteen described species) occurring thruout the Holarctic region. Four species are found in eastern North America. None of the American species have been reared. In Europe, the life history and morphology of *Dicranota bimaculata* (Schum.) has been discussed in detail by Miall (1893) and by Wesenberg-Lund (1915:342–343). Larvae were found by Miall in numbers in the muddy banks of small streams and ponds, where they bury themselves in the mud and gravel. They creep about with ease and rapidity between the sand and gravel, and are able to swim well by a looping movement. Their food consists largely of small worms, *Tubifex rivulorum* Lam., which abound in these haunts. The pupal stage is passed in damp earth. The larva is stated to be about 18 millimeters in length, but this seems to be a maximum figure. The body is dirty white in color and is covered with fine, appressed hairs. Abdominal segments 3 to 7 bear paired retractile pseudopods, which are circled with three rows of chitinized hooks gradually decreasing in size from the tips inward. The anal gills, four in number, are distinctly segmented. The head capsule is elongate and massive as in the tribe. The mentum is completely divided, its anterior margin having the usual six teeth. The mandible is of the usual pediciine type with acute teeth on the ventral cutting edge and a brush of hairs near the prosthecal region. (Plate LXIV.)

The pupa is small, only about 10 millimeters in length, and has the pronotal breathing horns expanded and flattened at the tips. The dorsal surface of the abdomen is provided with roughened plates armed with rather strong and dense spines, there being one such plate on the third segment, two on the fourth to sixth segments, and one on the seventh segment.

Genus **Rhaphidolabis** Osten Sacken (Gr. *needle + forceps*)

1869 *Rhaphidolabis* O. S. Mon. Dipt. N. Amer., part 4, p. 284–287.
1911 *Claduroides* Brun. Rec. Indian Mus., vol. 6, p. 288.

Rhaphidolabis is a small genus, including about fifteen described species ranging thruout the North Temperate Zone. The larvae strongly resemble those of Dicranota, and the two genera are undoubtedly very closely related.

Rhaphidolabis tenuipes O. S.

1869 *Rhaphidolabis tenuipes* O. S. Mon. Dipt. N. Amer., part 4, p. 287.

Needham (1908a:212–214) found adult flies of the species *Rhaphidolabis tenuipes* in great numbers in tent traps set over Beaver Meadow Brook in the Adirondacks in July and August, 1907. Larvae that almost certainly belong here were found among the rounded stones in the creek bottom.

Larva.— Length excluding caudal lobes, 8–9 mm.
Length of caudal lobes, 1 mm.

Abdominal segments 3 to 7 with prominent fleshy prolongations on ventral surface, these being retractile, unpaired, and widely separated on mid-ventral line, and bearing at tip a circlet of outcurved hooklets, with series of smaller hooklets beyond. Spiracular disk with the two ventral lobes long and obtuse at tips. (Further details are given by Needham.)

Rhaphidolabis cayuga Alex. (supposition)

1916 *Rhaphidolabis cayuga* Alex. Proc. Acad. Nat. Sci. Phila., p. 543–544.

Larvae which the writer refers to this species were found in Needham's Glen, Ithaca, New York, on March 30, 1916. Later in the season, in April and May, adult flies of the species are very numerous in this glen, and these account for the specific reference.

Larva.— Agreeing very closely with descriptions of both Dicranota and *Rhaphidolabis tenuipes.* Spiracles large, lying in a distinct longitudinal groove, by the closing of which they are capable of being entirely hidden. Antenna long and slender, tapering to apex, which bears numerous short papillae. Mandible with third lateral tooth of ventral cutting row very long and acute, much exceeding second tooth; basal tooth shaped like a pruning knife, with the cutting edge sinuate; at prosthecal region of mandible, a small tuft of about seven or eight long setae. Maxilla having the two lobes firmly united except on apical quarter.

Tribe Eriopterini

The tribe Eriopterini comprises a vast assemblage of usually small crane-flies whose geographical range is coextensive with that of the family.

The larvae, so far as known, are herbivorous. They show a remarkable uniformity in the structure of the head capsule. In the generalized members such as Molophilus and some Erioptera, the ventral bars of the head capsule are toothed at their anterior ends and form mental plates which are apparently homologous with those of the Pediciini. In Chionea an apparently similar condition exists, to judge from Brauer's figures. In the majority of species, however, the ventral bars of the capsule are not enlarged nor toothed anteriorly and do not function as the mental plates. The hypopharynx is preserved as a hemispherical cushion which is densely provided with setae. The mandibles are small and are blunt at their tips; the teeth of the cutting edge are usually three in numbe and blunt, but in some species (Ormosia, Gonomyia) they are longe and more prominent. A distinct prosthecal lobe or hook is usuall developed, and near the base of the mandible is a slitlike opening bearin a fringe of long, yellow setae. The maxillae are rather large, hairy lobes The labrum and epipharynx is long and narrow, and densely hairy. Th antennae are remarkably uniform thruout the group, consisting of a stou cylindrical basal segment with a slightly smaller apical papilla of a elongate-oval shape. In the Elephantomyaria the condition is somewha similar, the mandibles being very small, and the esophageal region bein conspicuously grooved with parallel lines and ridges. The spiracula disk is obliquely truncated and indistinctly lobed in Chionea and Teucho labis; surrounded by four lobes in Elephantomyia; squarely truncate and surrounded by four (in Rhabdomastix) or usually five lobes. I the undetermined Eriopterine No. 1, the five lobes are spatulate flattene blades with the margins hooked. Anal gills are usually present an variously developed in the different genera. The pupa is rather slende in the Elephantomyaria with the rostral sheath very long and the pal strongly recurved. The head usually bears a small setiferous crest whic is rarely lacking. The pronotal breathing horns vary considerably i form and relative size, being flattened into fans in some Gonomyia, sma and trumpet-shaped in other Gonomyia and in Gnophomyia, elonga in most species. The mesonotum is usually armed at the crest with spine hooks, or setiferous tubercles. The leg sheaths are very short in Gn

phomyia but are longer in other genera, and the middle tarsi are usually shorter than the other legs. The abdominal segments are subdivided into two rings, the posterior ring with a transverse row of spines and setae before the margin. The lateral spiracles are small, protuberant, and, in some cases at least, apparently functional. The dorsum of the eighth abdominal segment is provided with four or five lobes, which are in some cases (as in some Ormosia) spinous at the tips.

The writer has subdivided the tribe Eriopterini into two divisions: the Elephantomyaria, with Elephantomyia and presumably Toxorhina and Ceratocheilus, and the Eriopteraria, including the other Nearctic genera as known. It is probable that Cladura and its relatives will require a division when their immature stages are better known.

The genera of the tribe Eriopterini may be separated by the following keys:

Larvae

1. Spiracular disk surrounded by four lobes 2
   Spiracular disk not as above 3
2. Ventral lobes with a single powerful seta; coloration a saturated golden yellow; lives under bark .... *Elephantomyia* O. S. (p. 952)
   Ventral lobes fringed with short setae; coloration pale yellow; lives in earth. *Rhabdomastix* Sk. (p. 942)
3. Spiracular disk obliquely truncated, appearing indistinctly trilobed or without lobes .. 4
   Spiracular disk squarely truncated, surrounded by five lobes 5
4. Mandibles with eight teeth; mental plates with seven teeth; lives in earth. *Chionea* Dalman (p. 950)
   Mandibles with less than eight teeth; mental plates not toothed; lives under bark. *Teucholabis* O. S. (p. 945)
5. Spiracular disk ending in five flattened black plates which are finely toothed along their margins .... *Genus incertus*, Eriopterine No. 1 (p. 956)
   Spiracular disk not as above 6
6. Ventral plates of head capsule expanded and toothed at anterior ends 7
   Ventral plates not toothed as above 8
7. Ventral plates with four teeth; coloration yellow; spiracular disk large, very heavily marked with black .... *Molophilus* Curt. (p. 911)
   Ventral plates with five to eight teeth; coloration green; spiracular disk very reduced, almost unmarked .... *Erioptera* (*chlorophylla* O. S.) (p. 918)
8. Marks of all the lobes solidly black .... *Trimicra* O. S. (p. 932)
   Some *Ormosia* Rond. (p. 922)
   Some of the marks more or less split by a pale line 9
9. The three dorsal lobes solidly dark, the ventral pair split by a pale line 10
   All paired lobes split by a pale line 11
10. Coloration saturated yellow; anal gills bluntly rounded; lives under bark. *Gnophomyia* O. S. (p. 934)
    Coloration pale yellow; anal gills elongate; lives in earth. *Helobia* St. Farg. et Serv. (p. 928)
11. Lobes surrounding disk very stout, blunt; marks of lateral lobes surrounding spiracles and often suffusing disk .... *Gonomyia* Meig., subgenus *Leiponeura* Skuse (p. 939)
    Lobes surrounding disk longer; marks of lobes not so extensive 12

12. All the lobes with two lines 13
Dorsal lobe solidly dark .... Some *Ormosia* Rond. (p. 922)
13. No dark marks on disk between spiracles .... Some *Ormosia* Rond. (p. 922)
Dark marks between spiracles 14
14. Spiracular disk very small; two spots on disk ... *Erioptera* (*megophthalma* Alex.) (p. 915)
Spiracular disk large; four or six spots on disk .... *Helobia* St. Farg. et Serv. (p. 928)

Pupae

1. Rostral sheath very elongated; antennal sheaths lying across face of eye. *Elephantomyia* O. S. (p. 952)
Rostral sheath not elongated; antennal sheaths lying behind eyes 2
2. Leg sheaths very short, barely exceeding wings; crest of mesonotum smooth or nearly so. *Gnophomyia* O. S. (p. 934)
Leg sheaths longer, ending about one segment beyond end of wings; crest of mesonotum with spines or tubercles 3
3. Mesonotum at crest with numerous sharp spines; hind tarsi the longest, middle tarsi the shortest, fore tarsi intermediate in length .... *Helobia* St. Farg. et Serv. (p. 928)
Mesonotum and tarsal arrangement not as above 4
4. Mesonotum at crest with six to eight tubercles provided with numerous setae; breathing horns fanlike or trumpet-like .... *Gonomyia* Meig. (p. 938)
Mesonotum and breathing horns not as above 5
5. Mesonotum at crest with four sharp spines or two plates produced into spines 6
Mesonotum at crest without distinct prominent spines 8
6. Mesonotum at crest with four spines 7
Mesonotum at crest with a plate on either side split at tip into three or four teeth. *Ormosia* (*nubila* [O. S.]) (p. 923)
7. Crest of mesonotum with two large spines; pronotal breathing horns small, closely applied to thorax; lives under bark .... *Teucholabis* O. S. (p. 945)
Crest of mesonotum with four large spines; pronotal breathing horns long, slender, curved; lives in earth .... *Molophilus* Curt. (p. 911)
8. Abdominal pleurites with a transverse subterminal row of from eight to twelve spines or stout setae; dorsum of segment 8 with a pentagon of five lobes. *Ormosia* Rond. (p. 922)
Abdominal pleurites without such a row of spines or setae; dorsum of segment 8 with four or fewer lobes .... *Erioptera* Meig. (p. 914)

The most important literature on the tribe Eriopterini is as follows:

Molophilus bifilatus	Larva, general	Keilin, 1913:4. (Hypodermal glands.)
Molophilus obscurus	General	Beling, 1879 56.
Molophilus ochraceus	Larva, pupa	Beling, 1886:193–194.
Erioptera maculata	Pupa	Beling, 1879:49.
Erioptera flavescens	Larva	Beling, 1879:50.
Erioptera lutea	Larva, pupa	Beling, 1886:192–193.
Erioptera sordida	General	Beling, 1879:56.
Cheilotrichia imbuta	General	De Meijere, 1920:76.
Lipsothrix icterica	Larva, pupa	Beling, 1886:192.
Ormosia haemorrhoidalis	Pupa	Beling, 1879:48–49.
Ormosia haemorrhoidalis	Larva, pupa	Beling, 1886:191–192.
Ormosia lineata	General	Beling, 1886:202.
Ormosia nodulosa	General	Beling, 1886:202.
Ormosia nodulosa	General	Cameron, 1917:65.
Ormosia varia	Larva, pupa	De Meijere, 1916:201–204.

Helobia hybrida	Larva, pupa	Beling, 1879:50–51.
Helobia hybrida	Larva	Hart, 1898 [1895]:199–200.
Helobia hybrida	Larva, pupa	Malloch, 1915–17b:229–230.
Trimicra pilipes	Larva, general	Gerbig, 1913:161–163.
Gnophomyia rufa	Larva, pupa	Hudson, 1920:32–33.
Gnophomyia tripudians	General	Gamkrelidze, 1913, a and b.
Gnophomyia tripudians	General	Keilin, 1913:3. (Hypodermal glands.)
Gnophomyia tripudians	Larva	Keilin, 1913:4. (Hypodermal glands.)
Gnophomyia tripudians	General	Edwards, 1919 b.
Gnophomyia tristissima	Larva, pupa, general	Malloch, 1915–17b:230–231.
Gonomyia tenella	General	Beling, 1879:56.
Rhabdomastix schistacea	Larva, pupa	Beling, 1886:195.
Trentepohlia bromeliadicola	Larva, pupa, general	Picado, 1913:356–357.
Trentepohlia leucoxena	General	Alexander, 1915 b.
Trentepohlia pennipes	Larva, pupa, general	De Meijere, 1911:50–51.
Teucholabis complexa	General	Johnson, 1900.
Chionea araneoides	Larva, general	Brauer, Egger, and Frauenfeld, 1854.

Subtribe **Eriopteraria**

Genus **Molophilus** Curtis (derivation obscure)

1833 *Molophilus* Curt. Brit. Ent., p. 444.

Larva.— Form long and slender. Spiracular disk squarely truncated and surrounded by five subequal lobes; paired lobes of disk heavily lined with black; a black mark running proximad from spiracles; dorsal lobe with an oval black area. Head capsule long and narrow; ventral rods flattened; anterior ends expanded, four-toothed, to form mental plates. Labrum narrow, densely hairy. Mandible blunt at apex; ventral cutting edge with about four teeth; a single subapical dorsal tooth. Maxilla large and blunt. Antenna large; apical papilla elongate-oval, sculptured.

Pupa.— Cephalic crest setiferous. Pronotal breathing horns long and slender, sinuously curved. Mesonotum declivitous, at crest with four powerful teeth. Wing sheaths ending at about midlength of second abdominal segment. Leg sheaths ending at about midlength of fourth abdominal segment; tarsi of middle legs the shortest. Abdomen with spiracles on segments 2 to 7; dorsum of segment 8 with four blunt lobes.

Molophilus is a well-defined genus (including more than fifty species) of small and usually dull-colored flies, which are found practically thruout the world.

The adult flies frequent shaded situations and may be swept from rank vegetation in such places. The swarming habits of this group are discussed later under the specific accounts.

The immature stages of the various species are spent in wet earth. In Europe, *Molophilus obscurus* (Meig.) (Beling, 1879:56) and *M. ochraceus* (Meig.) (Beling, 1886:193–194) have been found in wet earth near running

water in shaded woods. The pupal duration of the latter species is no more than ten days. Keilin (1913:4) notes the presence of hypoderma glands in larvae of *M. bifilatus* Verr., but does not mention the larva habitat. Of the American species, *M. hirtipennis* has been reared fro similar situations.

Molophilus hirtipennis (O. S.)

1859 *Erioptera hirtipennis* O. S. Proc. Acad. Nat. Sci. Phila., p. 228.

The little dark-colored crane-flies of the species *Molophilus hirtipenni* are common on vegetation in shaded woods in spring and early summe or they may be found in small dancing swarms in similar situations.

The larvae are exceedingly abundant in wet organic mud or in cool, ric woods in the neighborhood of streams or springs. The writer has reare the species very frequently from specimens found in Needham's Gle and on Bool's hillside, Ithaca, New York, in April and May, 1914 t 1917. The pupal period is probably about a week, but in all the rearing of the writer this could not be ascertained closer than ten days.

Larva.— Length, 9–10 mm.
Diameter, 0.4–0.5 mm.

Coloration light yellow.

Form long and narrow; body terete, noticeably constricted before spiracular disk (Plat XLV, 344). Integument covered with a delicate appressed pubescence and a few transvers rows of very short, erect setae. Spiracular disk (Plate LXV, 351) squarely truncated, su rounded by five subequal lobes; ventral lobes on inner face with two heavy black parall lines, separated by a capillary yellow line; lateral lobes with a similar double line runni inward far beyond spiracle; these double lines not connected at distal end; dorsal lobe wit a single oval black mark which is less intense outwardly; a black mark beginning at spirac running proximad toward center of disk; lobes with a few short hairs at tips. (There is little variation in the degree of intensity, but the general pattern is as described above Anal gills four, short and blunt.

Head capsule (Plate LXV, 345) long, narrow, consisting of six chitinized rods, the ventr rods broad and flat, at the anterior end expanded to form the mental plates (Plate LXV, 346 each rod contributing four teeth, of which the outermost is bluntly rounded, the middle pa the largest and subequal. Dorsal bars two on either side, one slender, at their anteri ends articulating with a transverse chitinized rod; the various bars connected by a th membranous tissue. Labrum and epipharynx elongate, narrow, occupying the space betwee mandible and antenna on either side, the ventral face with abundant long hairs, on sid margined with numerous long, incurved, flattened setae. Mental plates as described abov behind them the hypopharynx (Plate LXV, 347), consisting of a semicircular cushion provide with dense, short setae. Antennae (Plate LXV, 348) rather closely approximated on dorsu prominent, each 1-segmented but bearing a long apical papilla; basal segment moderate elongated, cylindrical, the apex obliquely truncated, the papilla hyaline, gradually narrowe

oward tip, shaped somewhat like an ear of corn, the surface delicately sculptured; besides his papilla, two or three much smaller cylindrical ones. Mandible (Plate LXV, 349) slender, nding in a blunt rounded lobe; ventral cutting edge with four blunt teeth, the second from he base very tiny and connected with the third from the base (in some specimens the teeth re very blunt and rounded, so that the cutting edge appears crenulated or wavy); a single ooth on dorsal cutting edge, immediately behind apex; prosthecal region of mandible with longitudinal slitlike opening filled with a dense row of long setae. Maxilla (Plate LXV, 50) large and blunt, the outer lobe pale, roughly triangular, covered with numerous short airs, and with a few small sensory papillae near apex, surrounding palpus; inner lobe a ttle shorter, densely clothed and fringed with abundant long yellow hairs.

Pupa.— Length, 6.2–7.3 mm.
Width, d.-s., 0.7–0.8 mm.
Depth, d.-v., 0.8–1 mm.

Head, thorax, and appendages brown, when fully matured almost black; breathing horns ellowish; abdomen pale yellowish white.

Cephalic crest of moderate size, consisting of two conical lobes directed forward and bearing stout seta on anterior face; immediately in front of these, a smaller transverse crest lying etween antennal bases. Front rather broad. Labrum triangular; lobes of labium triangular, ivergent; maxillary palpi elongate, moderately stout, narrowed at tips and extending beyond oints of fore legs. Thorax prominent, carinate medially before declivity. Breathing orns long and slender, sinuously curved, apices directed forward. Declivity of mesonotum Plate LXVI, 352) precipitous, at the crest armed with four powerful teeth, median pair the rgest, somewhat divergent, separated by median line; a few tiny setae on mesonotum, includ-g four in a transverse row at about the level of wing root. Wing sheaths ending opposite pex of second abdominal segment. (In fully matured pupae the characteristic venation of his genus shows on the wing pads.) Leg sheaths rather short, ending about opposite mid-ngth of fourth abdominal segment; hind legs slightly the longest, fore legs a little shorter, iddle legs conspicuously shorter, ending about opposite apex of fourth tarsal segment of re legs.

Abdominal segments with two very narrow basal rings and a much broader posterior ng. Abdominal spiracles distinct on segments 2 to 7. Setae as follows: on pleura, one mmediately caudad of spiracle, a second caudad and somewhat dorsad of spiracle opposite osterior ring, another opposite anterior ring. Tergum with two setae on sides of posterior ng. Segment 8 with four blunt lobes on dorsum. Male cauda (Plate LXVI, 353 and 354) ith ventral lobe large, bluntly rounded at tips; dorsal lobes ending in two acute, chitinized oints which are widely separated and directed dorsad and slightly caudad, on outer face ith a small seta; near base of cauda on dorsum, surface tumid and bearing a small seta on ther side. Female cauda (Plate LXVI, 355 and 356) with sternal acidothecae much shorter an the very long tergal valves, these latter, just before apex, with an acute spine which is irected dorsad and with a seta on side. (When the pupa is nearly ready to transform the adult, the long, coarse bristles covering the body of the adult, and the chitinized enitalia, show thru the pupal integument.)

Nepionotype.— Ithaca, New York, May 11, 1917. No. 33–1917.
Neanotype.— Ithaca, June 1, 1917.
Paratypes.— About one hundred larvae and pupae from type locality.

Molophilus ursinus (O. S.)

1859 *Erioptera ursina* O. S. Proc. Acad. Nat. Sci. Phila., p. 228.

Molophilus ursinus is probably the smallest crane-fly in North America. The following notes on the swarming were made along Power House Creek, Gloversville, New York, on June 27, 1915:

This species occurred in small dancing swarms over the little lateral streamlets that poured down the steep slope, some of the swarms including scores of individuals. When not swarming, they rested flat on the upper surfaces of leaves, their wings folded over the abdomen. Crane-flies associated with this species today included the following: *Bittacomorphella jonesi*, *Limnophila toxoneura*, *L. areolata*, *L.* (*Lasiomastix*) *tenuicornis*, *Liogma nodicornis*, *Dolichopeza americana*, *Tipula collaris*, *T. nobilis*, *T. iroquois*, *T. hermannia*, *T. macrolabis*, *T. submaculata*, *T. fuliginosa*, *Nephrotoma macrocera*, *N. tenuis*, *Longurio testaceus*, and others.

Genus **Erioptera** Meigen (Gr. *wool + wing*)

1800 *Polymeda* Meig. Nouv. Class. Mouch., p. 14 (*nomen nudum*).
1803 *Erioptera* Meig. Illiger's Mag., vol. 2, p. 262.
1818 *Polyraphia* Meig. Syst. Beschr. Zweifl. Ins., vol. 1, p. 88.
1854 *Octavia* Bigot. Ann. Soc. Ent. France, p. 474.
1856 *Chemalida* Rond. Dipt. Ital. Prodr., vol. 1, p. 180.
1856 *Limnaea* Rond. Dipt. Ital. Prodr., vol. 1, p. 181.
1856 *Ilisia* Rond. Dipt. Ital. Prodr., vol. 1, p. 182.
1861 *Limnoica* Rond. Dipt. Ital. Prodr., Corrigenda, vol. 4, p. 11.
1863 *Trichosticha* Schin. Wien. Ent. Monatschr., vol. 7, p. 221.
1864 *Platytoma* Lioy. Atti dell' Institut Veneto, ser. 3, vol. 10, p. 42.

Larva.— Form elongate, in some cases very slender, terete. Spiracular disk tending to be reduced, in some species (as *E. chlorophylla*) very small. Anal gills blunt. Head capsule slender, consisting of six bars, four dorsal and two ventral; ventral bars in some species (as *E. chlorophylla*), at least, with five to eight teeth at their expanded anterior end, forming the mental plates. Labrum narrow, densely hairy. Mandible small, bluntly toothed. Maxilla blunt, hairy. Hypopharynx cushion-like.

Pupa.— Cephalic crest consisting of blunt or acute (in *E. chlorophylla* and *E. vespertina*) lobes. Pronotal breathing horns elongate, the length many times the diameter, usually straight and slightly divergent (*E. megophthalma*, *E. septemtrionis*), or acutely pointed and directed forward (*E. chlorophylla*). Mesonotal declivity along crest with very numerous setiferous tubercles or (in the European *E. lutea*) with four prominent teeth. Leg sheaths moderately long, reaching fourth abdominal segment; middle tarsi conspicuously shorter than the others. Subapical armature of abdominal segments strong on sternites and tergites but lacking on pleurites. Spiracles distinct, tubular. Lobes on dorsum of eighth abdominal segment not forming a distinct pentagon.

Erioptera is a large genus of small flies, including more than one hundred described species, chiefly from the temperate regions. In the case of all species of which the immature stages are known, these stages are spent in wet earth. In Europe, *Erioptera* (*Acyphona*) *maculata* (Beling, 1879

9) was found under leaves in damp earth in woods. Pupae taken on une 8, 1874, emerged as adults on the 13th. The species was found lso in the sandy mud of a small brook bed. *E.* (*E.*) *flavescens* (Beling, 879:50) was found in sandy, damp earth, *E.* (*E.*) *sordida* (Beling, 1879: 6, mention only) in wet, sandy earth along brooks, and *E.* (*E.*) *lutea* Beling, 1886:192–193) in woods, in damp hollows, and along the margins f brooks, usually under leaf mold. Edwards (1919 a) has recorded a pecies of Erioptera as being associated with the larvae of the mosquito 'aeniorhynchus at the roots of water grass (*Glyceria fluitans*) in ngland.

In America, *E. chlorophylla*, *E. vespertina*, *E. caloptera*, and other pecies inhabit wet mud in open swamps; *E. septemtrionis* and *E. megophalma*, rich organic mud in cool, shady woods; *E. armata*, *E.* near *nabi*, and other species, the soil along the sandy banks of streams. *E.* (*Acyphona*) *graphica* was considered by Hart (1898 [1895]:197) to be emiaquatic.

The writer has before him the larvae of only two species of the genus, *. chlorophylla* and *E. megophthalma*. These are readily separated by heir color, *E. chlorophylla* being pale green, *E. megophthalma* pale ellow and more elongate. The pupae of the Nearctic species of the enus may be separated by the following key:

Breathing horns and cephalic crest strongly pointed and curved forward at their tips; coloration light green................................*E. chlorophylla* O. S. (p. 918)
Breathing horns and cephalic crest not as above; coloration not green................2
Breathing horns elongate-cylindrical to slightly flattened, almost straight but slightly divergent, diameter subequal for entire length....................................3
Breathing horns not as above, more or less curved, or else blunt at their tips..........4
Cephalic crest sharply pointed; eyes large...............*E. megophthalma* Alex. (p. 915)
Cephalic crest not sharply pointed; eyes small............*E. septemtrionis* O. S. (p. 920)
Breathing horns almost straight, enlarged distally, tips blunt.
E. sp. (near *knabi* Alex.) (p. 922)
Breathing horns curved, narrowed toward tips......................................5
Breathing horns widely separated at base, bent strongly proximad, contiguous medially; lobes of cephalic crest acute, vertical; eyes large...........*E. vespertina* O. S. (p. 919)
Breathing horns curved gently forward; cephalic crest with lobes directed laterad, divergent; eyes of moderate size..............................*E. armata* O. S. (p. 921)

rioptera megophthalma Alex.

1918 *Erioptera megophthalma* Alex. Can. Ent., vol. 50, p. 60–61.

The adult flies of *Erioptera megophthalma* are not uncommon in ol, shaded, and boggy woods during the months of early spring.

They may be swept from rich vegetation in company with such char-acteristic species as *Limnophila brevifurca, L. fuscovaria, L. subtenuicornis Adelphomyia minuta, Rhaphidolabina flaveola, Molophilus hirtipennis Erioptera venusta, E. stigmatica, Gonomyia florens, G. subcinerea,* and *Tipula oropezoides.*

The elongate larvae of this fly were very common in rich organic mu taken from Bool's hillside, Ithaca, New York (as discussed under th account of *Bittacomorphella jonesi*, page 780), where they were associate with a crane-fly fauna characteristic of such situations. The larvae, i life, are pale yellowish, with the food contents, of a chalky white colo showing thru the integument. The head capsule and the spiracular dis are very small; the inner face of each lobe of the latter is very narrowl lined with black. The species was reared many times during late Ma and early June, 1917, the length of the pupal existence indoors being seve or eight days.

Larva.— Length, 10.4–11.6 mm.
Diameter, 0.7–0.75 mm.

Coloration very pale yellow; contents of alimentary canal chalky white.

Form terete, elongated, body tapering gradually to the posterior end, just beyond gi (Plate LXVII, 358) suddenly constricted; last segment elongate-cylindrical, tapering grad ally to the very small spiracular disk. Body covered with a short, appressed pube cence, on last segment this pubescence coarser and more erect, with a few elongate hai interspersed; lateral parts of body at caudal margins of segments with short transver lines of small, erect setae; a few other similar rows at about midlength of certain of t segments. Spiracular disk (Plate LXVII, 357) very small, tending to be eliminated reduction; lobes short and blunt, dorso-median lobe the smallest; ventral lobes with t short brown lines, not connected distally, the proximal line a little longer than the late line of each lobe; the pale space between these lines a little less than diameter of o lateral lobes with two similar divergent lines, the dorsal one attaining inner level spiracles; dorsal lobe with two small, indistinct, brown lines; on disk between spiracles t small round spots which do not touch spiracles; lobes fringed with short hairs near t and capable of close approximation so that disk is often entirely closed. Spiracles lar nearly circular.

Head capsule small, very long and slender, greatly dissected, the three bars of either s long and delicate; dorsal bars at their articulation joined with a short longitudinal bar n whose anterior end the antennae are inserted; ventral bars of capsule not conspicuou expanded at their anterior end, and apparently not toothed as in other species of this ge and in Molophilus. Labrum and epipharynx long and narrow, lying between anten bases; epipharyngeal region densely clothed with short setae at tip and with two para brushes on ventral face. Mentum apparently not formed as in *E. chlorophylla*, a sligh

rched transverse chitinized bar. Hypopharynx about as in Molophilus. Antennae rather losely approximated, directed cephalad; basal segment moderately elongated, cylindrical; pical papilla relatively small, elongate-oval. Mandible very small, with blunt teeth; pical point short, blunt; ventral row of teeth about three in number, often very blunt. Maxilla as in Molophilus, but outer lobe with the vestiture of hairs rather longer.

Pupa.— Length, 7.2–8.2 mm.
Width, d.-s., 0.8–0.9 mm.
Depth, d.-v., 1–1.1 mm.

Head light brown; thorax anterior to declivity conspicuously darker brown; remainder of body light yellowish brown; breathing horns light yellow. (In fully colored individuals the head and the thorax with their appendages become much darker, almost black, but the breathing horns retain their conspicuous yellow color.)

Head short, face tumid. Eyes of male very large, widely separated by front; eyes of female smaller. Cephalic crest consisting of two prominent lobes; viewed from side, these lobes sharply pointed and directed slightly forward, with a seta on outer ventral face before tips; viewed from front, lobes rounded, ending in acute tips, separated by a deep, rather narrow, V-shaped notch. Front between eyes narrowed toward labrum, which is rather sharply pointed. Labial sheaths small, the lobes contiguous with their apices truncated, the lateral angles obtuse or produced into a tiny lobe. Sheaths of maxillary palpi short and stout, tapering gradually to tips. Antennal sheaths moderately elongated, angulated at segments, ending just beyond base of wing. Pronotal breathing horns stout, expanded at base, almost straight and only slightly divergent, somewhat compressed, transversely wrinkled basally; a small setiferous tubercle in front of base of breathing horn. Mesonotum precipitous, at crest (Plate LXVII, 359) on either side of median line with abundant tiny setiferous tubercles bearing long, pale hairs, these tubercles continued back along shoulder. Lateral margin of thorax with two small setae. Wing sheaths ending before tip of second abdominal segment. Leg sheaths (Plate LXVII, 360) short, attaining base of fourth abdominal segment; tarsi of hind legs the longest, those of middle pair the shortest; fore legs with femora and tibiae very short.

Abdominal segments (Plate LXVII, 361) divided into two annuli by a constriction near midlength, the anterior ring very indistinctly subdivided further into two lesser annulets; on segments 4 to 7, before caudal margin of posterior ring on both dorsum and sternum, a transverse row of small, conspicuous, blackened, setiferous tubercles, which are more distant from one another near ends of rows; on basal abdominal segments these tubercles less evident but still present. Pleura with small but probably non-functional spiracles, which are very indistinct in young pupae but are more evident in fully colored individuals; these spiracles located near base of posterior ring. Setae on abdomen as follows: on sternal segments, one seta just caudad of end of row of spicules, a second at lateral end of this row, intermixed with spicules, two on posterior ring on a level with spicules; on tergal segments, a strong seta on a line with spiracles, another seta below end of row of spicules; on pleura, one seta just ventrad of spiracles, and two post-spiracular and one ante-spiracular setae. Male cauda (Plate LXVII, 362 and 363) with ventral lobes obliquely truncated, blunt at tips, projecting beyond level of subacute dorsal lobes; dorsal lobes slender, slightly divergent apically, blackened before tips and with two setae at tips on outer face; at base of cauda,

on dorsal face of eighth segment, a close quadrangle of four rounded tubercles, placed on a slight elevation. Female cauda with tergal acidothecae elongate, subacute at tips; sternal valves short, blunt; quadrangle of tubercles on dorsum of eighth segment more distinct than in the male.

Nepionotype.— Ithaca, New York, May 14, 1917.
Neanotype.— Ithaca, June 5, 1917.
Paratypes.— Larvae and pupae in large numbers from type locality, May 14 to June 5, 1917.

Erioptera chlorophylla O. S.

1859 *Erioptera chlorophylla* O. S. Proc. Acad. Nat. Sci. Phila., p. 226.

Erioptera chlorophylla is conspicuous by its pale green color in the larval, pupal, and adult stages. It is a common and widely distributed species thruout eastern North America. Several larvae were found in organic mud at Orono, Maine, on June 13, 1913, one of which pupated on the 21st. When the insect is dropped into boiling water, the green color immediately disappears. The associates of this species are discussed under the account of *Ptychoptera rufocincta* (page 775).

Larva.— Length, 9–10 mm.
Diameter, 0.7–0.75 mm.

Color uniformly pale green, fading to a pale yellow after death.

Form moderately elongated, last segment of body elongate, gradually narrowed to bluntly rounded apex. Body clothed with numerous appressed hairs. Spiracular disk somewhat as in *E. megophthalma* but even more reduced, disk usually entirely closed, lateral lobes on either side capable of close approximation, tracheae before the opening into spiracles very large.

Head capsule (Plate LXVIII, 364) of the Molophilus type, but longer and slenderer; the two dorsal bars of each side very delicate, the ventral bars broader and flattened. Mental plates (Plate LXVIII, 365 and 366) slender; anterior end of each ventral bar widely expanded and provided with several teeth; these teeth varying in number, in some specimens there being only five, in others eight, teeth to each plate; in the latter case the third from either side is larger, with two smaller teeth between. Hypopharynx about as in Molophilus. Antenna (Plate LXVIII, 367) large, basal segment stout, cylindrical; apical papilla elongate-oval, with apex bluntly rounded and surface weakly sculptured; laterad of this papilla a tiny cylindrical hyaline peg. Mandible (Plate LXVIII, 368) rather large; cutting edge with about four slender teeth, the second from base the smallest; dorsal face of mandible with a blunt subapical tooth and an oblique comb of about six stout setae or chitinized teeth. Maxilla similar to that of Molophilus, but the hairy vestiture longer and coarser.

Pupa.— Length, 8.8–9 mm.
Width, d.-s., 1.2 mm.
Depth, d.-v., 1.2 mm.

Breathing horns reddish brown; thoracic dorsum green, with a brownish tinge; abdomen uniformly pale green, posterior half of each dorsal segment a little darker.

Cephalic crest small and compact, consisting of two prominent but closely approximated lobes which are separated by a deep U-shaped notch, the tips acute and directed forward; on outer face before apex a short seta. Labrum broadly obtuse at tip. Labial lobes roughly triangular, divergent. Maxillary palpi short and stout, narrowed toward tip. Antennal sheaths with a slender tubercle at base above eye.

Pronotal breathing horns broad at base, narrowed to the acute tip which is directed almost ventrad; viewed from above, horns very broad basally and with a dorsal carina; ventral side at base transversely wrinkled; a small setiferous lobe just in front of breathing horns, directed laterad. Mesonotum behind breathing horns with a high compressed carina, on either side of this produced into a lobe directed cephalad and laterad; mesonotum moderately declivitous (Plate LXIX, 369), at crest with numerous setiferous tubercles which are fewer in number and more widely separated along shoulder. Leg sheaths reaching to about middle of fourth abdominal segment; hind legs a little longer than fore legs; middle legs very short, ending opposite base of last segment of fore legs.

Abdominal segments divided into two narrow basal rings and a broad posterior ring; on pleura a distinct spiracle, opposite posterior annulus and nearer dorsal margin; posterior annulus, before caudal margin, with a dorsal and a ventral row of long, stout setae. Setae on abdomen as follows: on pleura, a seta opposite second basal ring, a second ventrad of spiracle, and two setae caudad of spiracle, the posterior one a little more dorsal in position; on tergites, two stout setae lying transversely on the margin opposite spiracle, a third seta at end of terminal rows of bristles; on sternites, a group of two transverse setae on posterior ring, slightly below level of spiracle and rather widely separated by the broad midventral area. Female cauda (Plate LXIX, 370) with dorsal acidothecae short, distinctly upturned, and ending in a small, subacute tip; before apex with two very short setae; a short blunt tubercle near base of valves; ventral lobes short, their tips very blunt; dorsum of segment 8 with two blunt median tubercles, one immediately behind the other.

(Described from larvae taken in the Basin Swamp, Orono, Maine, June 13, 1913; one pupa with the larva, July 5, 1913.)

Erioptera vespertina O. S.

1859 *Erioptera vespertina* O. S. Proc. Acad. Nat. Sci. Phila., p. 226.

Erioptera vespertina is a characteristic inhabitant of open swamps and wet meadows. It has not been reared, but a pupa found in organic mud in the Basin Swamp, Orono, Maine, on June 24, 1913, undoubtedly belongs to this species. The associates are discussed under the account of *Bittacomorpha clavipes* (page 785).

Pupa.— Length, 8.5 mm.
Depth, d.-v., 1.1 mm.

Breathing horns reddish brown; thoracic dorsum reddish brown, with an interrupted whitish line running down posterior half of mesonotum; sheaths of wings and legs pale

brown; abdomen whitish yellow, posterior half of each sternite and tergite dark brown; basal half with two narrow transverse lines of same color.

Lobes of cephalic crest widely separated, subtriangular, acutely pointed at tips. Pronotal breathing horns cylindrical, transversely wrinkled, tapering gradually to tips. (In the only specimen at hand, the horns are widely separated at the base but soon bend proximad and thence outward and ventrad, so that the two horns are closely approximated or almost contiguous on their distal parts.) Behind breathing horns, mesonotum with conspicuous divergent lobes such as are described for *E. chlorophylla*; mesonotum at crest with abundant black setiferous tubercles, which are fewer in number, smaller, and more scattered along shoulder, interrupted at mid-dorsal line. Hind legs a little longer than fore legs, which, in turn, are a little longer than middle legs.

Abdominal segments with subterminal armature of posterior ring more spinous than in *E. chlorophylla*. Distribution of setae about as in *E. chlorophylla*.

(Described from a pupa taken at Orono, Maine, June 24, 1913.)

Erioptera septemtrionis O. S.

1859 *Erioptera septemtrionis* O. S. Proc. Acad. Nat. Sci. Phila., p. 226.

Erioptera septemtrionis is a widely distributed species thruout the northeastern United States and Canada. The larvae are not uncommon in rich organic mud in cool, shaded woods. The writer found them commonly in the Standpipe Woods, Orono, Maine, in July and August, 1913. A larva placed in rearing on July 3 transformed to an adult female on the 16th. Other larvae placed in rearing on July 15 transformed to adult males on the 25th. This limits the pupal duration to not more than ten days, but it is probably much less, presumably about one week.

Pupa.— Length of cast skin, 7 mm.

Cephalic crest low and flat. Antennal sheaths moderately elongated, individual segments showing clearly thru sheaths. Pronotal breathing horns elongate, cylindrical, almost straight but slightly diverging, transversely wrinkled, paler at tips, with a row of small breathing pores along apical margin; a few small setiferous tubercles before base of breathing horns. Declivity of mesonotum rather steep, at crest with numerous small tubercles and abundant pale yellow hairs which are less numerous along shoulder. Leg sheaths with middle pair conspicuously the shortest, as in the genus.

Abdominal segments with subterminal armature of posterior ring consisting of stout pale setae; arrangement of these setae about as in *E. chlorophylla*. Lateral spiracles distinct. Male cauda (Plate LXIX, 371 and 372) with the ventral lobes blunt at tips, obliquely truncated, separated by an acute V-shaped notch; dorsal lobes separated by a U-shaped notch, each lobe terminating in a small tip, with two tiny setae on lateral face before apex; dorsum of eighth segment with four prominent, pale, fleshy lobes which are closely approximated, the anterior pair directed laterad and a little more distant from each other than the posterior pair, which are directed more dorsad.

Neanotype.— Orono, Maine, July 25, 1913. No. 105-1913.

(Subgenus **Hoplolabis** Osten Sacken)

1869 *Hoplolabis* O. S. Mon. Dipt. N. Amer., part 4, p. 160.

The subgenus Hoplolabis includes but three known species — the type of the group, *Erioptera (Hoplolabis) armata*, discussed below; *E. (H.) bipartita* O. S., of western North America; and *E. (H.) asiatica* Alex., of Japan.

Erioptera (Hoplolabis) armata O. S.

1859 *Erioptera armata* O. S. Proc. Acad. Nat. Sci. Phila., p. 227.

Erioptera armata is a rather common fly thruout the northeastern United States. A larva was found in the sand along the banks of Fall Creek, Ithaca, New York, on May 16, 1917. This larva was of the typical eriopterine form, being elongate, terete, and with the spiracular disk surrounded by five subequal lobes. It was placed in rearing and transformed to an adult female on May 31. This larva was found associated with numerous hexatomine larvae, such as *Eriocera spinosa*, *E. longicornis*, and *E. cinerea*.

The following description is from the cast pupal skin.

Length, about 7 mm.

Cephalic crest consisting of two moderately large, slightly divergent lobes which are acutely pointed at tips; lobes directed strongly outward and bearing a seta on outer face. Labrum acutely pointed. Labial lobes large, divergent, almost straight across caudal margin. Sheaths of maxillary palpi stout, rather pointed at tips. Pronotal breathing horns broad at base, tapering to slender apices, bases conspicuously wrinkled; a small setiferous tubercle before base of each breathing horn. Mesonotum at crest (Plate LXIX, 373) with numerous short, chitinized points. Lateral angle of thorax with two setae; a strong seta above wing axil. Leg sheaths with middle tarsi ending conspicuously before tarsi of other legs.

Each abdominal segment before posterior margin with a transverse row of slender black spicules or short bristles on tergum and sternum, and smaller areas on pleura. Lateral abdominal spiracles distinct. Setae on pleura just ventrad of spiracle, and on tergum just above transverse row of spicules. Female cauda with tergal valves elongated, gently upcurved, unarmed; sternal valves shorter, blunt; at base of cauda, on dorsum of eighth segment, four small darkened tubercles which are produced into slender tips.

Neanotype.— Cast pupal skin, Ithaca, New York, May 31, 1917.

(Subgenus **Mesocyphona** Osten Sacken)

1869 *Mesocyphona* O. S. Mon. Dipt. N. Amer., part 4, p. 161.

Mesocyphona is one of the larger subgenera of Erioptera, reaching its maximum of specific development in the Tropics of the New World.

The immature stages of *Erioptera* (*Mesocyphona*) *caloptera* (Say) and *E.* (*M.*) *parva* O. S. are spent in wet mud along the banks of streams and other bodies of water. The species discussed below as *Erioptera* (*Mesocyphona*) species (near *knabi*), was reared from the sandy margins of a small prairie stream in Kansas.

Erioptera (*Mesocyphona*) species (near *knabi* Alex.)

Adult flies of a small species of Mesocyphona which is close to *E.* (*M.*) *knabi* Alex., of Mexico, were not uncommon along Buckner Creek, a small prairie stream flowing thru Jetmore, Kansas. These adults, especially the females, were photophilous, appearing in considerable numbers around lanterns which were hung in tents pitched along the banks of this stream. A single pupa found in the muddy sand along the bank of the creek on July 20, 1917, emerged as an adult on the 22d. The following general characters of the species may be noted:

Pupa.— Labrum small, apex rather sharp. Labial lobes squarely truncated, with lateral angles subacute. Sheaths of maxillary palpi slender. Pronotal breathing horns moderately long, cylindrical, curved slightly forward, enlarged outwardly, blunt at tips. Mesonotum at crest rather tumid and with a few long hairs inserted on stout black tubercles. Leg sheaths with middle tarsi the shortest, hind tarsi the longest.

Neanotype.— Jetmore, Hodgeman County, Kansas, July 22, 1917.

Genus **Ormosia** Rondani (Gr. *chain*)

1856 *Ormosia* Rond. Dipt. Ital. Prodr., vol. 1, p. 180.
1860 *Rhypholophus* Kol. Wien. Ent. Monatschr., vol. 4, p. 393.
1863 *Dasyptera* Schin. Wien. Ent. Monatschr., vol. 7, p. 221.

Larva.— Form terete, moderately elongated. Spiracular disk squarely truncated, surrounded by five subequal lobes which are lined with double marks of brown. Anal gills blunt. Head capsule slender, very dissected, of six narrow bars, four dorsal and two ventral, the ventral bars broader. Labrum narrow, epipharynx hairy. Mandible with teeth moderately elongated. Antenna of the Molophilus type. Mentum without chitinized teeth.

Pupa.— Cephalic crest setiferous. Pronotal breathing horns rather short and stout, more or less flattened and with a row of tubercles along posterior margin. Mesonotum declivitous, at crest with a flattened, toothed, chitinized plate on either side (in *O. nubila*) or with abundant setiferous tubercles. Wing sheaths ending opposite or just beyond tip of second abdominal segment. Leg sheaths varying in length with the different species, middle tarsi the shortest. Abdominal segments with a subterminal transverse row of spines or setae, these occurring on pleura (as small groups of eight to twelve) as well as on tergites and sternites. Lateral spiracles distinct, on segments 2 to 7; dorsum of segment 8 with

a pentagon of five lobes, these being unarmed (*O. innocens, O. meigenii*) or spinous-tipped (*O. nubila, O. nigripila*).

Ormosia is a large and rather difficult genus (including more than seventy-five species) of small crane-flies which are characteristic of subarctic and temperate regions and apparently rare or lacking in the Tropics.

The adult flies occur in small dancing swarms, usually in cool, shaded situations in or near woods or along brooks. They are most numerous in early spring and in late summer or early autumn, many of the species being apparently double-brooded.

The immature stages are spent in moist organic mud near water. In Europe, Beling records *Ormosia haemorrhoidalis* (Zett.) (Beling, 1879: 48–49, and 1886:191–192), *O. lineata* (Meig.) (Beling, 1886:202), and *O. nodulosa* (Macq.) (Beling, 1886:202), as being found in wet earth in woods, usually beneath leaf mold. Cameron (1917:65) likewise records the last-named species as living in mud. *O. varia* (Meig.) was found by De Meijere (1916:201–204) among decaying leaves in a wet spot near a ditch.

Of the American species, the writer has bred *Ormosia innocens, O. nubila, O. meigenii*, and *O. nigripila* from larvae or pupae in entirely similar situations to those given above for the European species.

The larvae of only two of these species, *O. nubila* and *O. meigenii*, are available to the writer at this time. *O. nubila* is a large brown species; *O. meigenii* is much slenderer, and is light yellow in color.

The pupae of the known Nearctic species may be distinguished as follows:

1. Dorsum of eighth abdominal segment with a pentagon of five lobes which are spinous at their tips 2
   Dorsum of eighth abdominal segment with a pentagon of five fleshy lobes 3
2. Crest of mesonotum with a flattened chitinized plate on either side of median line. *O. nubila* (O. S.) (p. 923)
   Crest of mesonotum tumid, with abundant coarse, yellowish setae on either side of median line . . . . . . *O. nigripila* (O. S.) (p. 927)
3. Abdomen with large, rectangular, dusky areas on posterior annuli of segments 2 to 8, giving abdomen a banded appearance; pleural setae rather numerous. *O. innocens* (O. S.) (p. 925)
   Abdomen without such dusky areas; pleural setae few in number. *O. meigenii* (O. S.) (p. 928)

Ormosia nubila (O. S.)

1859 *Erioptera nubila* O. S. Proc. Acad. Nat. Sci. Phila., p. 227.

Ormosia nubila is probably double-brooded, since the flies are on the wing in the spring and again in the fall. The immature stages live in

organic mud that is usually covered over with a layer of leaf mold. On March 27, 1914, the writer found four large brown eriopterine larvae in rich earth from Needham's Glen, Ithaca, New York. An adult female of the present species emerged on April 9. This makes the maximum pupal existence less than two weeks, but it is undoubtedly very much less than this.

Larva.— Length, 11.5–11.8 mm.
Diameter, 1.1–1.2 mm.

Color a deep reddish or cinnamon brown; incisures of segments paler.

Form rather stout, body terete. Skin covered with a short, appressed pubescence. Spiracular disk (Plate LXX, 375) squarely truncated, surrounded by five subequal lobes; ventral lobes with two parallel dark brown lines which are narrowly united distally, the pale stripe between rather broad, distinct, especially near center of disk; lateral lobes with two parallel dark brown stripes which are indistinctly connected distally, the space between dusky with numerous brown spots; dorsal lobe with an elongate-oval mark inclosing a linear yellow center; lobes fringed with long hairs which are longest at tips, shorter toward base, and narrowly interrupted between lobes; disk between spiracles unmarked. Spiracles large; middle piece and extreme outer margins of ring blackish; spiracles separated by a distance about equal to one and one-half times diameter of one.

Head capsule about as in Molophilus, but ventral bars of capsule not toothed to form the characteristic mental plate of that genus. Labrum and epipharynx about as in Molophilus. Hypopharynx broad, flattened, provided with numerous transverse rows of short setae. Antenna short; basal segment stout, cylindrical; apical papilla rather small, elongate-oval. Mandible (Plate LXX, 374) ending in a rather long apical point, with about four long, flattened teeth along ventral cutting edge, the second from base very small; a short recurved hook at prosthecal region and a dense tuft of long yellow hairs in prosthecal slit; a dorsal appendage at heel of mandible. Maxilla about as in Molophilus.

Pupa.— Length, 7.5 mm.
Width, d.-s., 1.2 mm.
Depth, d.-v., 1.4 mm.

Head, thorax, and appendages pale yellow; breathing horns yellow; chitinized plates on mesonotum dark brown; abdomen brown. (In mature pupae, the sheaths of the appendages are probably darker.)

Cephalic crest (Plate LXXI, 381) low; lateral angles produced into conical, erect spinous tubercles, each bearing a stout seta on outer ventral face. Antennal sheaths very angulated, almost serrate. Opposite each segment of antenna on basal half of organ, a conspicuous blackened tubercle, those at base larger and more conspicuous, the lateral one directed outward, above it a second tubercle directed cephalad and simulating a crest. Antenna extending to just beyond base of wings. Front broad; a blackish area on either side near inner margin of eye, probably indicating point of attachment of tentorium. Labrum triangular, apex subacute. Labial lobes triangular, tips blunt. Sheaths of maxillary palpi rather long, narrowed to the slender tip. Pronotal breathing horns short and slender, some

what flattened, pale yellow; a stout seta just before base of each breathing horn. Mesonotum precipitous; at crest (Plate LXXI, 380) on either side of median line, a heavily chitinized flattened plate projecting dorsad; this plate, at its tip, forking into two lesser teeth, the lateral one of these still further subdivided into two still smaller teeth (in one specimen the left plate is divided dichotomously into four teeth, the inner primary tooth being further subdivided); on shoulder laterad of these plates a slightly swollen plate which is parallelly grooved; two spines on lateral angle of thorax above base of wing; mesonotum with a few setae behind crest, as follows: an anterior solitary seta on either side of median line and close to it, a solitary stout seta above wing axil, two groups of paired setae, one just dorsad of base of wing and the other midway between this group and the anterior seta first described. Wing sheaths rather short, ending opposite base of third abdominal segment. Leg sheaths rather long for this genus, ending opposite midlength of fifth abdominal segment; fore tarsi a little shorter than hind tarsi, middle tarsi very short, ending opposite or just beyond end of third tarsal segment of fore legs.

Abdominal segments near posterior margin with transverse rows of short black spineg which are much smaller and more widely separated near ends of row; at intervals alona row a few elongate setae; on pleura a similar area of eight to eleven spines with a single sets in row; tubular lateral spiracles on segments 2 to 7. Chaetotaxy as follows: on pleura, just above dorsal end of row, one seta, another solitary seta cephalad of spiracle on anterior ring; on tergites, a solitary seta on posterior ring about opposite spiracle; on sternites, two small setae on either side of median line of posterior ring. Female cauda (Plate LXXI, 382) with tergal valves long and slender, almost straight but slightly upcurved near tips; on dorsal lateral margin, just before tip, a prominent tooth directed laterad and slightly caudad; about midlength of valves a somewhat similar blunt tubercle on either side near dorsal margin; at base of eighth tergite a pentagon of five chitinized lobes, the anterior one rudimentary, the four developed lobes ending in acute chitinized points and each bearing a subapical seta; anterior pair of lobes more widely separated and bearing on lower side near base a small, slender lobule.

Nepionotype.— Ithaca, New York, March 27, 1914.
Neanotype.— Ithaca, with type larva, April 9, 1914. No. 2-1914.
Paratypes.— With types.

Ormosia innocens (O. S.)

1869 *Rhyphoiophus innocens* O. S. Mon. Dipt. N. Amer., part 4, p. 142.

Ormosia innocens is a characteristic early spring species, the adult flies being found in late April and during May. On May 12, 1917, a few pupae in an advanced stage of development were sifted from organic mud from Bool's hillside, Ithaca, New York. One of these emerged as an adult on the following day. The associated crane-fly larvae that occurred with this species on the date named were as follows: *Bittacomorphella jonesi*, *Dicranomyia stulta*, *Limnophila adusta*, *L. fuscovaria*, *Ulomorpha pilosella*, *Penthoptera albitarsis*, *Rhaphidolabina flaveola*,

Molophilus hirtipennis, Erioptera megophthalma, Ormosia nigripila, Tipula oropezoides, T. collaris, T. cayuga.

Pupa.— Length, 7.5–10.5 mm.
Width, d.-s., 0.8–1 mm.
Depth, d.-v., 1–1.2 mm.

(The smaller measurements are those of males, the larger those of females.)

Head and thorax brown; mesonotum before declivity darker brown; abdomen pale yellowish white, the sternal and tergal sclerites with broad, rectangular, darker areas, producing a banded appearance; breathing horns pale yellow. (In older pupae, the coloration of the head and the thorax is much darker.)

Cephalic crest of moderate size, bilobed; viewed from side, lobes blunt, with two lateral setae; viewed from front, lobes separated by a very broad, V-shaped notch. Between antennal bases, forehead longitudinally grooved, these lines converging between eyes. Labrum triangular, subacute, separating the small labial lobes. Maxillary palpi of moderate length, tapering to blunt apices. Antenna of moderate length, reaching to just beyond wing base. Pronotal breathing horns rather short and stout, almost straight and only slightly diverging, subcylindrical, compressed, and slightly constricted just beyond base. Mesonotum precipitous, carinate medially; at crest (Plate LXX, 376) with numerous pale hairs, these narrowly interrupted on median line; lateral angle of thorax with two tiny setae; a strong seta slightly dorsad and cephalad of wing root; about four small setae in alinement across mesonotum. Wing sheaths moderately broad, ending at or just before tip of second abdominal segment. Leg sheaths short, tips of all the tarsi ending about on a level, or those of fore legs a little longer, terminating just before end of third abdominal segment.

Abdominal segments divided into two distinct annuli by a constriction at about midlength of segment; sternum and tergum of posterior ring of segments 2 to 8 near caudal margin with large, rectangular, dusky areas which appear subchitinized; caudal margin of this area with a fringe of long, black hairs, there being about seventy-five of these on intermediate segments; on pleural membrane a very small, similar area bearing from twenty-five to thirty-nine hairs, and near its dorsal margin a distinct black tubular spiracle on segments 2 to 7; the following additional setae on segments: on dorsal segments, rectangular darkened areas with sparse scattered elongate hairs over surface, and two setae on each anterior ventral angle, their arrangement oblique; sternal segments similar, but the two setae on rectangular area arranged transversely; just caudad of ends of fringe of hairs, one or two isolated hairs; pleural membrane opposite basal annulus with a single seta; another seta opposite posterior annulus near ventral margin; a third seta on ventro-cephalic angle of pleural setiferous area just above level of spiracle; segment 8 on dorsum with five pale, gill-like lobes arranged in a quadrangle or a pentagon, the anterior lateral pair the longest, the median one rather the smallest; at base of anterior pair, two setae on cephalic face; at base of posterior pair, a single seta on lateral face. Male cauda (Plate LXX, 377 and 378) terminating in two very blunt ventral lobes and two separated, slender, dorsal lobes projecting caudad and dorsad. Female cauda similar to male cauda, but tergal acidothecae very elongate, much longer than sternal valves.

Neanotype.— Ithaca, New York, May 12, 1917.
Paratypes.— Seven pupae, with type.

Ormosia nigripila (O. S.)

1869 *Rhypholophus nigripilus* O. S. Mon. Dipt. N. Amer., part 4, p. 142.

The larvae of *Ormosia nigripila* are common in rich organic mud in shady places. Larvae found in Needham's Glen, Ithaca, New York, on March 27, 1914, emerged on April 18. Other larvae from Coy Glen, found on April 17, emerged on May 1. At Orono, Maine, large larvae were found on July 14, 1913, and were placed in rearing, emerging on the 26th as adult males. This limits the pupal duration to not more than two weeks, but it is undoubtedly much less, probably not more than a few days or a week.

Pupa.— Length, 5.2 mm.
Width, d.-s., 0.9 mm.
Depth, d.-v., 1 mm.

Head, thorax, and appendages light brown, becoming darker in maturity; breathing horns and abdomen pale whitish.

Cephalic crest with lobes small, low, and rounded, with a powerful seta at tip, directed forward. Labrum blunt at apex. Labial lobes large, subtriangular, lateral angles obtusely pointed. Sheaths of maxillary palpi stout, rather elongate. Pronotal breathing horns (Plate LXXII, 384) rather short and flat, compressed, slightly expanded beyond base; outer, or posterior, margin with about five small tubercles, at least one of which is setiferous. Mesonotum very steep and precipitous, as in this group of species; crest (Plate LXXII, 383) tumid, extensive, on either side with abundant coarse yellow bristles; caudad of these, four stout setae in a quadrangle, two on either side of median line; lateral angles of thorax with two stout setae; a strong seta just above wing base. Wing sheaths reaching base of third abdominal segment. Leg sheaths moderately long, extending almost to midlength of fourth abdominal segment; tarsi of middle legs much shorter than the others, hind legs a very little longer than fore legs.

Abdomen with segments (Plate LXXII, 385) before their caudal margin bearing transverse rows of slender spines; pleura with a small area lying a little cephalad of tergal and sternal rows and margined behind with eight to ten spines. Spiracles distinct, tubular. Setae as follows: on pleura, a seta on anterior annulus, a stout seta just ventrad of spiracles, and a third lying a little ventrad and cephalad of spiracle; on sternites, two stout setae near base of posterior annulus; on tergites, two setae on posterior annulus, lying transversely at level of spiracle, and a third seta just cephalad of end of row of spines. Male cauda (Plate LXXII, 386) with ventral lobes rather slender, narrowed outwardly, and somewhat pointed at apex; dorsal lobes curved strongly backward, terminating in acute, chitinized points with a strong seta on outer face before tip and a second seta nearer base; dorsum of segment 8 with five brown, chitinized lobes which are crowned at their apices with a circlet of spines; posterior pair the longest and stoutest, broad at base, more slender outwardly, with a large lateral spine and about three smaller inner spines; anterior pair more slender; median lobe slender, crowned with a circlet of about six small, subequal spines. Female cauda (Plate

LXXII, 387) with dorsal terebra elongate, almost straight or very slightly upturned; eighth segment with dorsal pentagon of spine-tipped lobes quite as in male.

Ormosia meigenii (O. S.)

1859 *Erioptera meigenii* O. S. Proc. Acad. Nat. Sci. Phila., p. 226.

Ormosia meigenii is one of the commonest species of the genus, occurring in small dancing swarms in early spring. Larvae of this species were taken on April 10, 1914, in organic mud from Needham's Glen, Ithaca, New York. An adult female emerged on May 4.

Larva.— Length, 6.5 mm.
Diameter, 0.5–0.6 mm.

Color, light yellow.

Form elongate, terete. Spiracular disk (Plate LXX, 379) about as in *O. nubila*, dorso-median lobe the smallest, ventral lobes with brown lines rather close together, the distal line the broadest; lateral lobes with lines rather short, not contiguous at their distal ends and not extending past midlength of spiracles; dorso-median lobe with marks oval, solidly dark brown. Lobes fringed with moderately long, yellowish setae, which are almost lacking at extreme tips; disk between spiracles unmarked. Spiracles large, transversely oval, separated by a distance a little greater than the long diameter of one.

Head capsule and mouth parts almost as in *O. nubila;* mandible with the long, slender teeth of that species.

Pupa.— (Described from a cast skin.)

Cephalic crest consisting of low, rounded lobes, each with a seta on anterior lateral face. Pronotal breathing horns of moderate length, flattened, a little narrowed toward tip, outer margin with fine tubercles. Mesonotum not so declivitous as usual in the genus, with tiny roughenings at crest; the usual two setae at lateral angle of thorax present, another above each wing, and four more in a transverse row at level of axilla of wing; a seta on mesonotum, close to median line, just below crest. Middle legs much shorter than fore and hind legs.

Subterminal rows of setae on abdominal segments consisting of slender, acute spines, with a few setae interspersed; on pleura the spines few in number. Spiracles elongate, tubular. Female cauda with tergal sheaths very long, sternal sheaths short, their tips blunt; on dorsum of eighth abdominal segment five small unarmed tubercles, which are blunt or nearly so, anterior pair more widely separated than posterior pair. (In the shape of the cephalic crest, the breathing horns, and the declivity of the mesonotum, this species resembles *O. nigripila;* but the arrangement of setae on the abdomen, and the great reduction and unarmed condition of the lobes on the eighth abdominal tergite, are distinctive.)

Nepionotype.— Ithaca, New York, April 10, 1914.
Neanotype.— Cast pupal skin, Ithaca, May 4, 1914.

Genus **Helobia** St. Farg. et Serv. (Gr. *marsh* + *I live*)

1825 *Helobia* St. Farg. et Serv. Encyclop. Method. Ins., vol. 10, p. 585.
1830 *Symplecta* Meig. Syst. Beschr., vol. 6, p. 282.
1865 *Idioneura* Phil. Verh. Zool.-Bot. Ges. Wien, vol. 15, p. 615.
1886 *Symplectomorpha* Mik. Wien. Ent. Zeitung, vol. 5, p. 318.

Larva.— Form moderately elongated, body terete. Spiracular disk surrounded by five subequal lobes which are marked with V-shaped brown lines, in some specimens the inner faces of the three most dorsal lobes being entirely brownish black. Anal gills moderately elongate. Head capsule as in the Eriopterini. Antenna with the apical papilla very short, subpyriform.

Pupa.— Cephalic crest setiferous. Pronotal breathing horns elongate-cylindrical, directed ventrad and cephalad, with rows of breathing pores along dorsal face. Mesonotum declivitous, at broad crest armed with numerous chitinized spines; an arcuated longitudinal row of six small pits extending from wing axil toward crest of thorax. Wing sheaths ending before tip of second abdominal segment. Leg sheaths ending about opposite tip of third abdominal segment; tarsi of hind legs the longest, those of middle legs the shortest, fore legs intermediate in length. Abdominal segments with a strong subterminal armature on ventral segments, much weaker to lacking on dorsal segments; lateral spiracles distinct on segments 2 to 7; dorsum of segment 8 with five blunt lobes.

Helobia is a small genus (five species) of common and sometimes very widely distributed crane-flies. The only North American species, *Helobia hybrida*, is apparently the most widespread tipulid known, ranging over practically the entire Holarctic region, southward in the mountains to India, and, in the New World, to Central America. The immature stages of the known species are spent in moist earth near water. Bruch (*in litt.*) mentions the rearing of *H. macroptera* (Phil.) in Argentina.

Helobia hybrida (Meig.)

1804 *Limonia hybrida* Meig. Klass., vol. 1, p. 57.
1818 *Limnobia punctipennis* Meig. Syst. Beschr. Zweifl. Ins., vol. 1, p. 147.
1830 *Symplecta punctipennis* Meig. Syst. Beschr. Zweifl. Ins., vol. 6, p. 283.
1848 *Limnobia cana* Walk. List Dipt. Brit. Mus., vol. 1, p. 48.

Helobia hybrida is undoubtedly the most widely distributed North American crane-fly. Beling (1879:50–51) found larvae and pupae at the end of July, 1876, in wet, sandy earth along the margins of small brooks in deciduous woods. Adults emerged in his breeding cages on July 27 and August 6. Hart (1898 [1895]:199–200) found the larvae in similar sandy situations along the Illinois River, associated with the larvae of *Tabanus atratus* Fabr. He suggests that it may serve as food for this horse-fly larva. Larvae of Helobia were especially abundant on May 17, and these transformed to adults within a month. Females were observed ovipositing along the shore, patting the valves of the ovipositor against the moist sand. Malloch (1915–17b:229–230) has given additional notes on the structural details of Hart's material.

Dr. Adam Böving found this species in Iceland and made careful notes on the burrows made by the larvae. Thru the kindness of Dr. Böving, the writer is able to include a translation of his manuscript. The writer is indebted also to Dr. Lundbeck, director of the museum at Copenhagen, for the loan of this material for study. These are the specimens discussed later in this paper. Böving's notes were made at Fell Station, southeast Iceland, in 1908. The translation follows:

Inside the moraine of 1877, in the low land where ice was standing in 1886, quantities of dipterous larvae were found in the moist sand on the bottom of flat hollows which at times are flooded by water and at times are partly drained, as was the case on the day when the following observations were taken.

The whole dark, moist surface of the bottom was covered by an irregular system of slightly elevated, long, tubular galleries, some of which were rather straight, some formed broken lines, some peculiar arabesques, and some plain spirals. The width of the galleries was about the size of an ordinary pinhead, some a trifle larger, some a little smaller. In the anterior part of each gallery was found either a cylindrical white tipulid larva (Helobia) about one centimeter long, or another dipterous larva of the same general size and appearance. The larvae were found just below the surface. It was not always easy to capture them, for when I pushed my knife under the mouth of the gallery they moved quickly backward, and then, digging deeper into the soil, made a new gallery that branched off from the main one. It was not possible to distinguish the galleries of the crane-fly larvae from those of the other dipterous associate. Very often, from the mouth of the spiral galleries, one-third of a broken pupal skin stuck out; but larvae were found also in many of these galleries.

The imagines of the two Diptera were present in large numbers, some flying close to the ground, others resting on it. Both forms were long-legged and capable of running over the water film. I secured a pair of both in copulation. The eggs were found on the moist surface, singly or in small masses of two or three together.

The larvae feed, of course, on organic particles in the sand. The imagines were not observed to take any nourishment at all; they copulated as soon as they had left the pupal skins, and I did not find them in any other place than on the bare, moist soil where the larvae lived; not, for instance, on flowers growing near by.

A small carabid (probably *Bembidion grapii* Gyll.) was present in the locality in comparatively large numbers, evidently preying on the larvae of the Diptera. A single carabid larva also was found; from its size and habitus it may very well be the larva of the Bembidion.

A small black spider was probably feeding on the imagines of the Diptera. It did not make a regular web, but spun a number of single threads, each about two feet long, attaching them to a piece of gravel and proceeding from this as a common center, spreading the threads close to the ground like radii, and finally fastening the ends to small grains of sand.

The adult flies of *Helobia hybrida* are very common. They are the first tipulids to appear on the wing in spring, some appearing in early March or, in open winters, even in late February. They remain until late in the fall. The writer has noted the females running about on the wet sand along the banks of the Kaw River at Lawrence, Kansas, and ovipositing quite as described by Hart (1898 [1895]: 199–200).

Larva.— Length, 7.8–10 mm.
Diameter, 0.6–0.7 mm.

Coloration, pale brownish yellow.

Form moderately elongated. Body covered with a sparse appressed pubescence. Spiracular disk (Plate LXXIII, 388) surrounded by five lobes, the dorsal one notably smaller than the paired lobes; inner face of lobes with two subparallel brown lines, connected at their outer ends to form narrow V's; disk marked with about six spots between spiracles, the largest at base of ventral lobes; disk fringed with short hairs, which are interrupted for a short distance between lobes. Anal gills moderately elongated, pale. (Beling describes the three dorsal lobes of the disk as having the entire inner face shiny blackish brown, and the ventral lobes merely margined with brownish; there would thus seem to be some variation in the character and degree of markings in this species.)

Head capsule as in the tribe. Antenna with the basal segment stout, cylindrical, the apical papilla very short, subpyriform. Mandible flattened; teeth large but very bluntly rounded; apical tooth the largest, with a slightly smaller denticle on either side.

Pupa.— Length, 7–9 mm.

Cephalic crest small; lobes pointed, directed ventrad, each bearing a short, stout seta. Labrum narrow. Labial lobes large, divergent, caudal margin almost straight across. Sheaths of maxillary palpi slender, narrowed at tip (Plate LXXIII, 390). Antenna moderately angulated, ending just beyond base of wing. Pronotal breathing horns elongate-cylindrical, directed ventrad and cephalad, with rows of breathing pores along dorsal face; ventral face transversely wrinkled. Mesonotum moderately declivitous, at broad crest (Plate LXXIII, 389) armed with numerous black chitinized spines directed backward; these spines most numerous proximally, interrupted by a median space, less numerous along shoulder; four setae in a transverse row across mesonotum, two on either side of median line; lateral angle of thorax broad and blunt, with two small setae, the outermost one the larger, the inner one about half its size; an arcuated longitudinal row of about six pits extending from above axil of wing toward crest of mesonotum. Wing sheaths short, ending before tip of second abdominal segment. Leg sheaths ending opposite or slightly beyond tip of third abdominal segment; hind legs much the longest, middle legs much the shortest, fore legs intermediate (Plate LXXIII, 391).

Abdomen with a rather strong armature of stout black spines on sternal segments, on segment 3 this appearing as a small area of about ten spines, on either side of tips of hind tarsi; tergal armature much weaker or lacking; lateral spiracles very distinct, tubular, in cast pupal skin the principal tracheal trunks being very conspicuous. Female cauda (Plate LXXIII, 393) with tergal valves the longest, terminating in sharp cylindrical points; sternal valves much shorter, blunt at tips; dorsum of segment 8 with five blunt lobes. Male cauda (Plate LXXIII, 392 and 394) with dorsal valves the longest, each terminating in a long, subacute, chitinized spine directed dorsad and laterad and bearing before its tip two stout setae; ventral lobes stout and blunt, longer than dorsal lobes.

Nepionotype.— Fell, between Öraefa and Heineberg, southeastern Iceland.
Neanotype.— Cast pupal skin, with type.
Paratypes.— Numerous cast pupal skins, with types (in the collection of the Copenhagen Museum).

Genus **Trimicra** Osten Sacken (Gr. *three* + *small*)

1861 *Trimicra* O. S. Proc. Acad. Nat. Sci. Phila., p. 290.

Trimicra is a small genus of crane-flies, including about fifteen described species found in most parts of the world, almost all being forms of moderate size and obscure coloration. These various species bear a close resemblance to one another and are hard to distinguish specifically.

Bergroth and other European writers consider the genus Trimicra as being the same as Psiloconopa Zetterstedt, but at this time the writer is not entirely willing to accept this view.

Beling (1879:48) described what he took to be the larva of one of these flies, and in his key to the larvae of crane-flies (1886:206) he included it in close proximity to the Pediciini. As mentioned elsewhere in this paper, it is highly probable that Beling described a pediciine larva, but by an accident had larvae of Trimicra in his breeding jars, the latter larvae emerging first and confusing the author.

Gerbig (1913:161–163) describes the real larva of *Trimicra pilipes* (Fabr.), the best-known species of the genus. It is found along the margins of flowing streams with muddy banks. It is a dark-colored larva, about 15 millimeters in length and about 2 millimeters in diameter. The skin of the body is similar to that of the larvae in the typical subgenus of the genus Limnophila, being covered with chitinous, hairlike projections, which in Trimicra are longest on the dorsal surface of the body. On each segment there are solitary elongate bristles, above and below each of which is a gland. The spiracular disk (Plate LXXIII, 395) is surrounded by five nearly equal lobes, which have the inner faces marked with equal blackened, chitinized areas. On the lateral margins of each lobe, but occupying only the distal part of the lobe and not continuous around the disk, is a fringe of moderately long hairs. At the tip of each ventral lobe are two bristles, and at the tip of each lateral lobe is a single bristle, these being inserted outside the line of hairs and surrounded by a bright circular area. The ventral sensory bristles found in some crane-fly larvae (as *Tipula variipennis*) are lacking. At the base of the lateral lobes are the spiracles, which are generally similar to those in the subgenus Limnophila. Gerbig discusses in detail the structure of the spiracles, the felt chamber, and the musculation of this region of the body.

Bruch (*in litt.*) mentions the rearing of *Trimicra reciproca* (Walk.) in Argentina from larvae very similar to that described above, occurring in the same type of habitat.

Genus **Empedomorpha** Alexander (Gr. *Empeda* + *shape*)

1916 *Empedomorpha* Alex. Proc. Acad. Nat. Sci. Phila., p. 507–508.

Empedomorpha is a monotypic genus of flies, evidently related to Trimicra. It is very curious in its marked sexual dimorphism, the male having an extremely large, hairy stigma, which encroaches upon the adjoining veins and often distorts them. The fly is still very insufficiently known. It is a prairie-inhabiting species, occurring from South Dakota to Texas and New Mexico. Nothing is known concerning the immature stages, and the following observations on the habits and occurrence of the adult flies are all that are available.

Empedomorpha empedoides (Alex.)

1916 (?) *Trimicra empedoides* Alex. Can. Ent., vol. 48, p. 44–45.

Empedomorpha empedoides, as stated under the generic account above, is a prairie-inhabiting species. Adult flies were found running about on the sand flats of the Arkansas River, near Cimarron, Kansas, from July 13 to 15, 1917, by H. L. Fackler and the writer. The vegetation of the sand bars here is very sparse to almost lacking, a few psammophytic grasses being the main element. Associated with these flies on the sandy surface were a characteristic group of sand-loving insects, of which the following were the most constant: larvae and adults of tiger beetles, representing at least three species of Cicindela; ground beetles, Carabidae, including such genera as Omophron, Dyschirius, Bembidion, Tachys, and a few others; rove beetles, Staphylinidae, such as Stenus; Heteroceridae, Psammocharidae, Asilidae, Saldidae, and similar groups. In the cool of early evening, numerous small spiders that lurk in hollows and in deserted insect burrows during the day emerge from hiding and become active.

The crane-flies were observed during the hours of bright sunlight, when the temperature registered over 100° F. in the sun. They run rapidly over the moist sand, their course being very shifting and zigzag, quite like that of tiger beetles. They fly readily but only for short distances, and prefer to alight on the sand rather than on the vegetation. They walk awkwardly over the sand, but are able to crawl up grass blades or

similar objects. The habits of the adult flies are strikingly like those of Helobia (page 930). The writer is sure that the larvae are to be found in the sand in these same haunts.

Genus **Gnophomyia** Osten Sacken (Gr. *darkness* + *fly*)

1859 *Gnophomyia* O. S. Proc. Acad. Nat. Sci. Phila., p. 223.
1867 *Furina* Jaenn. Abhandl. Senkenb. Ges., vol. 6, p. 318.
1911 *Dasymallomyia* Brun. Rec. Indian Mus., vol. 6, p. 304.

Larva.— Body slender, tapering toward ends, with transverse welts on intermediate abdominal segments. Spiracular disk surrounded by five subequal lobes. Anal gills consisting of four blunt, rounded lobes, constructed for propulsion rather than for a respiratory function. Head capsule moderately elongated, rather compact for the Eriopterini. Antenna rather small, apical papilla elongate-oval. Mandible slender, with a long apical point and three teeth along ventral cutting edge.

Pupa.— Cephalic crest a low, blunt tubercle on either side of median line, each tipped with a long seta. Pronotal breathing horns small, narrowly trumpet-shaped. Mesonotum moderately declivitous, at crest practically unarmed; a strong seta at lateral angle of thorax and another on either side of mesonotum behind crest. Wing sheaths short, ending before tip of second abdominal segment. Leg sheaths very short, reaching just beyond wings, attaining end of second abdominal segment; all the tarsi ending about on a level. Abdomen provided with long setae; spiracles on abdominal segments 2 to 7.

Gnophomyia is a small genus including about forty described species which are most abundant in the Tropics of the New World. The European *Gnophomyia tripudians* Bergr. has recently been reared by Gamkrelidze (1913, a and b) and by Keilin (Edwards, 1919b). The former found larvae in large numbers in the viscous, semi-decomposed mass of tissue beneath the bark of a fallen carolina poplar, associated with *Miastor metraloas* Meinert. These larvae were found near Paris, France, in March, 1911. Gamkrelidze records a gregarine parasite in the intestine and a nematode worm in the body cavity. The species was later reared in England from dead oak by Keilin, who has discussed and figured glands in the larvae (1913:3). The only American species that has been reared is the common *Gnophomyia tristissima,* discussed later.

Gnophomyia rufa Hudson, of New Zealand, has recently been discussed in some detail by Hudson (1920:32–33). It is occasionally found in dense forests in the vicinity of Wellington. The larva lives in and feeds on the semi-liquid vegetable detritus which accumulates in large quantities at the bases of the leaves of *Astelia Solandri*, a common and very conspicuous epiphytic plant in most of the primitive native forests. The length of

the fully grown larva is slightly over 30 millimeters. It is subcylindrical, considerably flattened. Oval warts armed with minute teeth are situated on both surfaces of abdominal segments 2 to 7. The larva is very dark slaty gray in color, darker toward the extremities. The spiracular disk as shown by Hudson's colored figure is very small. Apparently only one larva inhabits the space between the two sheathing leaves of the Astelia, and only those leaves which are full of a thick, brown, coffee-like liquid are frequented. The pupa is inclosed in a rather tough, extremely elongate, silken tube situated between the sheathing leaves. It rests in an upright position in the midst of the semi-liquid mass. The pupa measures about 38 millimeters in length, being very elongate with the head and the thorax unusually small. The two pronotal breathing horns are shaped somewhat like a bivalve shell. Abdominal segments 3 to 6 at the base on the dorsal side have finely-toothed warts; the ventral surface has plain ridges. It is probable that the present species is not a true Gnophomyia, but until more is known of this species and its relatives it should be referred to this genus.

The *Gnophomyia pilipes* referred to by Beling (1879:42) and by Gerbig (1913:161–163) pertains to Trimicra (page 932).

G. tristissima has been recorded by Malloch (1915–17b:230–231) as living in wet mud, but this is an error. The writer has material from exactly the same source as Malloch's, received from James A. Hyslop, and this shows that the haunt of the larvae is beneath the decaying bark of trees — an unusual habitat for one of the Eriopterini, which for the most part live in damp sand or earth near water. The rearing of this species in New York (by Young), Massachusetts (by Johnson), Maryland (by Hyslop), Virginia (by Shannon), Kansas (by Alexander), Illinois (by Malloch and Alexander), and Texas (by Mitchell), leaves no question that the immature stages are to be found beneath the decaying bark of the larger hardwood trees, the tulip tree, *Liriodendron Tulipifera* Linn., being often preferred.

Gnophomyia tristissima O. S.

1859 *Gnophomyia tristissima* O. S. Proc. Acad. Nat. Sci. Phila., p. 224.

Gnophomyia tristissima is an interesting black fly with conspicuous yellow halteres. It is common and widely distributed thruout the eastern

United States and Canada. As stated above, the species has been reared on at least seven different occasions in as many States, the most complete account being that by Hyslop, whose specimens and manuscript notes were kindly placed at the writer's disposal. His data on this species are as follows:

May 14, 1914. Wolfsville, Maryland. Under the bark of a rotten stump of a tulip poplar (Liriodendron) on the roadside near Warrenfeltz schoolhouse, field on the left going to town. I found a great number of amber-yellow dipterous larvae (three in alcohol), and also three pupae slightly shortened and with the thorax and legs ferruginous and the abdomen pale amber. They were in a very moist nidus of rotted inner bark; placed in rearing in a tin box.

May 16. One adult emerged today (pinned); pupal case in alcohol.

May 18. Three adults emerged today (pinned); pupal cases in alcohol. Observed emergence of one adult. The swaying motion observed in *Tipula infuscata* was not observed, but the adult simply glided straight out of the pupal case by a wavelike contraction of the abdomen. The whole emergence took only about eight seconds. A larva pupated.

May 23. Adult emerged. Pupal stage five days. Placed the remainder of the pupae (all had transformed from larvae to pupae) in alcohol. The pupae are quite active and move under a shelter if exposed. Just before emerging, the pupa takes on a black color on the thorax and smoky yellow on the abdomen.

Shannon's material was reared from pupae taken under the bark of a dead tulip tree at Dead Run, Fairfax County, Virginia, on May 5, 1913. A larva that is undoubtedly this same species was found beneath the same tree on April 17, 1913. Johnson bred this species from larvae found beneath bark at Riverside, Massachusetts, on April 24, 1905. The Texas specimens were found by Mitchell beneath the bark of cottonwood (Populus) at Victoria, on June 30.

At Lawrence, Kansas, in 1919, the writer found a few larvae under the bark of a box elder, associated with the following dipterous larvae: *Pterocalla strigula* Loew, *Lonchaea laticornis* Meig., *Phaonia harti* Mall. These associated species were kindly determined by Mr. Malloch. In 1920 the flies were bred from under the bark of several deciduous trees at Urbana, Illinois, by Mr. Malloch and the writer.

Well-preserved specimens of the larvae are not available to the writer, and the following description is taken direct from Malloch (1915–17 b: 230–231):

Larva.— Length, 9–11 mm. Slender, slightly tapering toward both extremities, more decidedly towards the cephalic. Body yellowish testaceous, covered with dense decumbent pile.

Head [Plate LXXIV, 396] more compact than that of Helobia, the lateral rods stouter; antennae very small; maxillae large, produced beyond the apex of the narrow labrum, the palpi stout; labium not chitinized; mandibles slender, with a long sharp apical tooth and about three poorly defined teeth along the lower lateral margin. Locomotor organs consisting of rather

broad fusiform areas on anterior portion of abdominal segments except basal and apical; hairs along margins of segmental incisions more distinct than elsewhere because of their being slightly curved upward; apical segment with five processes, their structure and markings as in figure [Plate LXXIV, 397]; anal ventral blood-gills in the form of four short rounded protuberances.

The pupa is described from four cast skins, kindly presented by Mr. Hyslop:

Pupa.— Length, 8–10 mm.

Cephalic crest a low, blunt tubercle on either side of median line, each tipped with a long, stout seta. Labrum broad, elongate, obtuse at tip, completely separating triangular labial lobes. Sheaths of maxillary palpi moderately slender, tapering gradually to tip. Antennal sheaths moderately elongated, extending to about opposite wing root; basal segments angulate. Pronotal breathing horns (Plate LXXIV, 399 and 400) small, trumpet-shaped, very flattened, median area lacking and hence the margins contiguous; just proximad of breathing horns a large, roughly triangular lobe on either side, immediately behind which are two small setae. Mesonotum moderately declivitous, at crest rather tumid, but unarmed, with a few parallel grooves on either side of median line; lateral angle of thorax very sharp, before tip with two setae, one very powerful, the more dorsal one abortive; a strong seta on either side of mesonotum behind crest. Wing sheaths short, ending just before tip of second abdominal segment. Leg sheaths (Plate LXXIV, 398) very short, ending just opposite tip of second abdominal segment and thus projecting but slightly beyond wing tips; hind legs a little the shortest, but no striking difference in length of various sheaths.

Abdominal segments subdivided into a narrow basal ring and a much broader posterior ring; abdominal segments on dorsum with four transverse rows of tiny but stout setae, two on basal ring and two on posterior ring, one being subbasal, the other subterminal, in position; sternum with only the subterminal row of setae present, but this well marked, the other rows merely vestigial; on either side of dorsum, just cephalad of ends of subterminal row of setae, a powerful bristle; in alinement with these and subequally spaced, two smaller setae; a strong pleural seta on a raised papilla opposite basal ring and three opposite posterior ring, the two anterior being larger, the posterior one very small; sternum with a strong seta on extreme lateral margin of posterior ring; lateral spiracles distinct, on segments 2 to 7. Male cauda (Plate LXXIV, 401) with ventral lobes small, blunt, rather widely separated basally but converging apically; dorsal lobes powerful, divergent, and rather acute at tips; at base of each near lateral margin a short bifid knob sending one arm dorsad, the other laterad; at base on cephalic angle a short, stout seta; two long, powerful, lateral setae on either side, and a single powerful seta on either side of dorsum, immediately behind which is a blunt tubercle. Female cauda with sternal valves elongate, powerful, at their tips terminating in slender, divergent points; dorsal valves small, blunt, divergent, located at base of sternal valves, at their tips with a short, slender spine directed backward; base of segment about as in male.

Neanotype.— Wolfsville, Maryland, May 16, 1913. No. 234.
Paratypes.— Two male and one female pupae from type locality, May 18, 1913.

Genus **Gonomyia** Meigen (Gr. *angle* + *fly*)

1818 *Gonomyia* Meig. Syst. Beschr. Zweifl. Ins., vol. 1, p. 146.
1856 *Taphrosia* Rond. Dipt. Ital. Prodr., vol. 1, p. 182.
1869 *Goniomyia* O. S. Mon. Dipt. N. Amer., part 4, p. 176.

Larva.— Form elongate, terete. Spiracular disk surrounded by five blunt lobes which are heavily marked with brown, in some species (*G. alexanderi*) the brown suffusing the disk between the spiracles. Head capsule of eriopterine type. Mandible with lateral teeth slender, flattened. Antenna with apical papilla elongate-oval. Mentum not chitinized.

Pupa.— Cephalic crest blunt, the surface with minute roughenings. Pronotal breathing horns flattened, fanlike (*G. sulphurella*), or short, trumpet-shaped. Mesonotum declivitous, at crest with an interrupted transverse row of six to eight tubercles which are densely beset with sharp black spicules. Wing sheaths attaining base of third abdominal segment. Leg sheaths moderately elongated, reaching base of fourth abdominal segment; tips of middle tarsi ending a short distance before apices of other tarsi. Armature of abdominal segments weak. Lateral spiracles distinct, tubular. Five blunt, fleshy lobes on dorsum of eighth abdominal segment.

Gonomyia is a large and diverse genus of small crane-flies (including more than one hundred known species) described from all parts of the world. They are divided into four recent subgenera, of which three — Gonomyia Meig., Progonomyia (new name for Gonomyella Alex., preoccupied), and Leiponeura Skuse — occur in the Nearctic fauna.

The immature stages of the known species are spent in moist sand or earth, usually near water. In Europe, *G. tenella* Meig. (Beling, 1879:56, mention only) was found in August in damp, sandy earth along the margin of a dried-up brook.

The writer has found the immature stages of *Gonomyia* (*Leiponeura*) *alexanderi* and *G.* (*G.*) *kansensis* in wet sand near rivers. *G. sulphurella* and *G. subcinerea* O. S. occur in muddier and more stagnant conditions near ponds and small streams.

Not enough larvae are available for study to require a key at this time. The pupae of the known Nearctic species may be distinguished by the following key:

1. Pronotal breathing horns narrow at base, expanded distally into a very flattened, fanlike blade with delicate and anastomosing nervures.......*G. sulphurella* O. S. (p. 940)
   Pronotal breathing horns not as above, more earlike or trumpet-shaped...............2
2. Pronotal breathing horns massive, trumpet-shaped; lateral margin of thorax before wing root produced into an angle; male cauda small, elongate, dorsal lobes a little shorter than ventral lobes, with two stout lobes on dorsal side far removed from their base...*G. alexanderi* (Johns.) (p. 939)
   Pronotal breathing horns flattened, earlike or narrowly trumpet-shaped; lateral margins of thorax above wing root broad and blunt; male cauda short, stout, dorsal and ventral lobes subequal in length, the latter closely approximated along median line, the former widely separated, at their base with two acute points.......*G. kansensis* Alex. (p. 941)

(Subgenus **Leiponeura** Skuse)

1889 *Leiponeura* Skuse. Proc. Linn. Soc. N. S. Wales, ser. **2**, vol. **4**, p. 795.
1915 *Lipophleps* Bergr. Psyche, vol. 22, p. 55.

Gonomyia (*Leiponeura*) *alexanderi* (Johns.)

1912 *Elliptera alexanderi* Johns. Psyche, vol. 19, p. 3.

The beautiful crane-fly *Gonomyia alexanderi* is locally common in the eastern United States. The adult flies may be swept from rank vegetation in the neighborhood of streams. When resting, the adults have a characteristic position, the fore legs standing straight ahead and almost parallel, the middle legs extended laterally and slightly forward, the hind legs directed backward but widely divergent, and the wings folded over the back. This is the characteristic resting position for the genus. The larvae were found in some numbers in rather coarse sand, around small pools of water near the Sacandaga River, Fulton County, New York, on June 5, 1914. The adults emerged on June 16, giving a pupal period of not more than eleven days and presumably much less. The description and figures of the pupa are made from the cast pupal skin of the male.

Larva.— Length, 8.3 mm.
Diameter, 0.4–0.5 mm.

Coloration very pale yellow or yellowish white.

Form terete, elongated, slender. Body with a sparse, pale pubescence, at posterior margins of segments with a transverse erect ridge of stiff hairs. Spiracular disk (Plate LXXV, 403) large, flattened, almost pentagonal in outline, surrounded by five lobes; dorso-median lobe small, slender; paired lobes very short and blunt; margin between lobes almost straight or but feebly concave; when disk is partly closed, lobes appearing a little more prominent; ventral lobes a little larger than lateral lobes; lobes heavily suffused with brown; on ventral lobes a lateral dark brown line running dorsad to near spiracles, at its dorsal end connected across disk by a paler brown suffusion; proximal stripes of ventral lobes shorter and paler, above their inner ends with a small brown spot; lateral lobes almost entirely suffused with brown, this entirely surrounding spiracles and in some specimens entirely suffusing disk between spiracles, this mark bifid at its distal end; dorsal lobe indistinctly marked with very pale brown; disk margined with short, pale hairs which are not interrupted and are only a little longer at tips of lobes. Spiracles widely separated, the distance between them being three or four times diameter of one; spiracles yellow, centers pale brown.

Head capsule as in the tribe, the ventral bars broader than the slender dorsal bars, their inner ends not expanded or toothed to form the mental plate. Labrum-epipharynx moderately elongate, densely hairy. Mentum not chitinized; hypopharyngeal region a cushion, covered with delicate, short setae. Antenna as in this tribe, basal segment moderately elongate, densely hairy, apical papilla rather small, elongate-oval. Mandible (Plate LXXV, 402)

moderately large; apical point elongated, slender; ventral cutting edge with three flattened teeth, gradually smaller from outermost toward base; outermost tooth flattened, a little enlarged distally, about as long as apical point; basal tooth small, acute; a prosthecal appendage with a brush of hairs beneath it.

Pupa.— Length of cast pupal skin, about 5.5 mm.

Cephalic crest of two prominent lobes, blunt at tips, their surface granulated. Labial lobes blunt at tips. Sheaths of maxillary palpi moderately stout, tapering suddenly to sharp apices. Antenna with basal segment very angulated. Pronotal breathing horns (Plate LXXVI, 408 and 409) massive, short, trumpet-shaped, flattened laterally, and here margined with an elevated ridge, along which are scattered the rows of breathing pores; mouth of this trumpet wide. On thorax between breathing horns, large, rounded lobes which are minutely granulated. Declivity of mesonotum (Plate LXXVI, 407) somewhat precipitous, at the rather narrow crest with about six small tubercles which are densely beset with spicules; along shoulder a similar, but more elongate, transverse welt; lateral margin of thorax before wing root projecting out as a sharp angle with a seta at its base. Wing sheaths reaching end of second abdominal segment. Leg sheaths moderately long, attaining base of fourth abdominal segment; fore legs a very little longer than hind legs; middle legs much shorter, ending just beyond base of last tarsal segment of fore legs.

Abdominal segments divided into two narrow basal rings and a much broader posterior annulus. Armature of abdomen very weak. Male cauda (Plate LXXVI, 410 and 411) small, elongate; ventral lobes a little longer than the short, blunt dorsal lobes; on dorsal face near end of eighth segment, two stout lobes pointed at the tips which are directed dorsad and slightly caudad; eighth segment with a close pentagon of pale, slender lobes, the posterior pair larger and closer together than the anterior pair, the median lobe the smallest.

Nepionotype.— Sacandaga River, Fulton County, New York, June 5, 1914.
Neanotype.— With type larva.
Paratypes.— Two larvae with type.

(Subgenus **Gonomyia** Meigen)

Gonomyia (*Gonomyia*) *sulphurella* O. S.

1859 *Gonomyia sulphurella* O. S. Proc. Acad. Nat. Sci. Phila., p. 230.
1869 *Goniomyia sulphurella* O. S. Mon. Dipt. N. Amer., part 4, p. 180–181.

Gonomyia sulphurella is a handsome little crane-fly which is very common and widely distributed thruout the eastern and central United States. Larvae are not infrequent in mud along the banks of streams. The writer has bred this species from larvae sifted from sandy mud from the banks of Cascadilla Pond, Ithaca, New York, where they occur associated with numerous larvae and pupae of a tabanid (*Chrysops indus* O. S.), a stratiomyiid (*Odontomyia* sp.), and other forms. Larvae collected on May 14, 1913, emerged as adults on June 1. Adults have been reared as late as October 19 by E. A. Richmond.

Pupa.— Length of cast pupal skin, about 6.5–7 mm.

Cephalic crest small, blunt. Labrum triangular, apex obtusely rounded. Labial lobes subcircular, outer margin rounded. Sheaths of maxillary palpi short and stout, at apex suddenly narrowed (Plate LXXVII, 414). Antennal sheaths angulated at segments, the organ extending to beyond base of wing. Pronotal breathing horns (Plate LXXVII, 413) with extreme base expanded, the neck short, constricted, soon passing into a greatly expanded and very compressed disk, the whole suggesting a fan or certain polypores; margin of this disk entire or gently crenulated, and sloping from ventral side outward; surface finely nerved and reticulated. Mesonotum somewhat precipitous, crest (Plate LXXVII, 412) tumid, with rounded knobs arranged transversely along it, there being about eight isolated knobs and a more elongate one along shoulders, these knobs covered with minute blackened spicules. Lateral margin of thorax above wing root forming almost a right angle. Wing sheaths ending opposite base of second abdominal segment. Leg sheaths comparatively short, ending opposite base of fourth abdominal segment; fore legs a little the longest, middle legs conspicuously shorter than the others.

Abdominal segments divided into two narrow basal rings and a broad posterior annulus. Armature of abdominal segments weak, posterior ring with a narrow row of small black spines before caudal margin; on basal ring a broad band of microscopic scabrous points arranged in interrupted transverse rows, there being about seven or eight of these rows to a band. Spiracles small but distinct. Female cauda with tergal valves short, but little longer than sternal valves, slightly upturned, ending in short, cylindrical tips; near base with a small, blunt tubercle on either side; dorsum of segment 8 with five rather long, pale lobes, the anterior pair more slender and more widely separated than the posterior pair, which are sometimes closely approximated.

Neanotype.— Cast pupal skin, Ithaca, New York, October 19, 1915.
Paratypes.— Three pupae with type.

Gonomyia (*Gonomyia*) *kansensis* Alex.

1918 *Gonomyia kansensis* Alex. Can. Ent., vol. 50, p. 158–160.

Gonomyia kansensis is a prairie species of the *cognatella* group and appears to be common along the Arkansas and Kaw Rivers in Kansas. Living pupae were found at Larned on August 1, 1917, in sand along the banks of the Arkansas River, where they were associated with the typical sand-loving fauna, including Gelastocoridae, Saldidae, and Carabidae (Omophron, Dyschirius, Bembidion, and Tachys). The observation of a small ant preying on a living pupa of this fly is discussed on page 729.

Pupa.— Length of cast pupal skin, 6 mm.

Similar to *G. alexanderi* in most essentials but showing the following differences: antennal sheaths strongly angulate at segments; a tubercle on ventral face of antenna at base, and another at inner cephalic margin of eye.

Pronotal breathing horns (Plate LXXVII, 415 and 416) flattened, earlike or very narrowly trumpet-shaped, with a thick marginal ridge, the disk restricted. Lateral angle of thorax above wing root very broad and blunt, setiferous. Leg sheaths of fore and hind legs almost on a level, those of middle legs shorter, ending a little beyond midlength of last tarsal segment of fore legs. Male cauda (Plate LXXVII, 417 and 418) with dorsal and ventral lobes very short and blunt, subequal in length; ventral lobes closely approximated on median line; dorsal lobes widely separated at their base, with two small acute points directed strongly dorsad, divergent at their tips, each with two small setae on outer face near base; dorsum of segment 8 with five lobes, the anterior pair a little more widely separated than the posterior pair, the median lobe slender.

Neanotype.— Larned, Kansas, August 1, 1917.

Genus **Rhabdomastix** Skuse (Gr. *rod* + *whip*)

1889 *Rhabdomastix* Skuse. Proc. Linn. Soc. N. S. Wales, ser. 2, vol. 4, p. 828–829.

The genus Rhabdomastix includes nearly a dozen species, some of which have been previously described as Gonomyiae.

The immature stages of *Rhabdomastix schistacea* (Schum.) were found by Beling (1886: 195) in wet earth beside a stream in beech woods on May 6. The larva measures 6 millimeters in length; the greatest diameter is 0.8 millimeter. The body is strongly dilated in the anterior part and gradually narrowed behind. The integument is deep brownish yellow. The spiracular disk is short and blunt, and has four very small, tuberculate teeth, the lateral pair lying somewhat more cephalad than the more powerful ventral pair; spiracles small, circular, yellowish brown, separated by a distance about equal to four times the diameter of one. The pupa has the mesonotal declivity provided with an interrupted crossrow of small, unequal, chitinized teeth.

(Subgenus **Sacandaga** Alexander)

1911 *Sacandaga* Alex. Ent. News, vol. 22, p. 349–352.

Rhabdomastix (*Sacandaga*) *flava* (Alex.)

1911 *Sacandaga flava* Alex. Ent. News, vol. 22, p. 351–352.

Rhabdomastix flava is a curious fly which is apparently related to Gonomyia but represents a quite different offshoot of the Eriopterini. The writer believes that the larvae might be found in moist earth along streams, but at present they are quite unknown. The following notes

on the swarming habits of this species have been published (Alexander, 1912 a: 72–73):

On June 13, 1909, I found the species swarming [on Sport Island, in the Sacandaga River, New York] and made the following observations: The species came out at about 7.45 p.m. and at 7.51 p.m. began its flight in under an elm tree at the northeast end of the island. The flight was generally forward, but continually from side to side for a few inches. The flight was quite irregular, always toward the slight north breeze. The whole swarm would often move away and return, a little later, to the first place. It swarmed within four feet of the ground, generally much lower, averaging, perhaps, two feet. . . . The number of individuals participating in the swarm was about twenty. Other species swarming nearby at the same time were *Chironomus hyperboreus*, var. *meridionalis*, Joh., and the may-flies, *Ephemerella excrucians* Walsh, and *Siphlonisca aerodromia* Ndm.

Genus **Trentepohlia** Bigot (named after J. J. Trentepohl)

1854 *Trentepohlia* Bigot. Ann. Soc. Ent. France, p. 474.
1911 *Mongomioides* Brun. Rec. Indian Mus., vol. 6, p. 296.
1912 *Mongomella* Enderl. Zool. Jahrb., vol. 32, part 1, p. 61.

Trentepohlia is a tropicopolitan genus including about fifty-five described species arranged in six subgenera — Trentepohlia Bigot, Anchimongoma Brun., Mongoma Westw., Plesiomongoma Brun., Paramongoma Brun., and Neomongoma Alex. Of these species, fifteen are American and the remainder are Old World forms. They are almost all species of delicate, ethereal structure, with long, slender legs. It is an interesting fact that *Trentepohlia* (*Mongoma*) *pennipes* has been observed by Jacobson (De Meijere, 1911: 50, and Edwards, 1912–13: 211) to form chains on horizontal spider webs, as is noted herein for Thrypticomyia (page 712) and somewhat similarly for Oropeza (page 982). H. K. Munro has supplied (*in litt.*) the following interesting notes on the habits of *Trentepohlia* (*Trentepohlia*) *humeralis* Alex. as observed in eastern Transvaal at the end of April, 1920:

Very inconspicuous when flying and resting. When flying resembles very much a small piece of thistledown. Invariably settles on under side of twigs, leaves, and similar objects. Usually found among bushy undergrowth, but also in grass. When at rest the wings are folded along back; very often on settling the insect moves itself up and down in the manner of the long-legged harvest spiders (Phalangiidae). Slow flier.

A fossil Trentepohlia, *T. cruciferella* (Ckll.), has been described from the Gurnet Bay Oligocene (Cockerell, 1917 b: 373–374). Observations on the immature stages of three species are available.

(Subgenus **Mongoma** Westwood)

Trentepohlia (*Mongoma*) *pennipes* (O. S.)

1887 *Mongoma pennipes* O. S. Berl. Ent. Zeit., vol. 31, part 2, p. 204.

The immature stages of *Trentepohlia pennipes* have been described by De Meijere (1911:50–51) as follows: Jacobson found the larvae at Semerang, Java, in January, 1906, in decaying plant stems. The only larva sent was 9 millimeters long and almost 1 millimeter in diameter, of cylindrical form, only slightly narrowed behind and brownish in color. The head capsule was entirely retracted. The entire body was thickly beset with fine, short, appressed hairs; in addition to these, on the ventral side of each of the six intermediate segments were transverse swellings where the hairs were shorter and even more numerous. Surrounding the anus were four long, cylindrical, anal gills, each constricted in three or four places; if bent forward, the anterior pair would reach the middle of the penultimate segment of the body, the posterior pair being somewhat shorter. The last segment of the body was truncated, the lower angles being somewhat produced and provided with a few somewhat longer hairs; the spiracles, situated in the upper part of the spiracular field, were relatively small and somewhat elongated.

The pupa (Plate LXXVIII, 419) was about 9 millimeters long, elongate, of a yellowish brown color, the abdomen for the most part brighter. The thorax was almost smooth, with only a few short, brownish yellow bristles. The abdomen, except on the anterior segments, was thickly set with numerous tubercles. The apex of the abdomen had two short, thornlike projections, curved outwardly; beneath these were two shorter tubercles, and four short tubercles formed a quadrangle on the dorsum of the last segment. The pronotal breathing horns consisted of flattened, leaflike lobes, the upper surface of which was scaly.

(Subgenus **Paramongoma** Brunetti)

Trentepohlia (*Paramongoma*) *bromeliadicola* (Alex.)

1912 *Mongoma bromeliadicola* Alex. Ent. News, vol. 23, p. 415–417.

Trentepohlia bromeliadicola and *T. leucoxena* have a larval habitat which has not been found elsewhere in the family. They live in the water that gathers in the leaf axils of tropical bromeliaceous plants,

spending their immature stages in this habitat, where they are associated with a remarkable fauna of other organisms. The adult females have the valves of the ovipositor greatly elongated, and the writer has suggested elsewhere that this may be an adaptation for laying the eggs in this habitat. *T. bromeliadicola* was reared in Costa Rica by Picado, whose important paper (Picado, 1913) on the bromeliaceous epiphytes contains colored figures of the larva, the pupa, and the adult. From this paper it is seen that the larva (page 356, figure A, and plate 13, figure 4, of reference cited) is not unlike that of *T. pennipes*, described above, the four prominent anal gills of *T. bromeliadicola* (Plate LXXVIII, 420, of this paper) being a notable feature in common, altho here the constrictions are very numerous, there being twenty-five or thirty shown in the figure. The pupa (Picado, 1913:357, fig. 51, and pl. 13, fig. 2) has the pronotal breathing horns (Plate LXXVIII, 421, of this paper) approximated on the median line, and the sheaths of the ovipositor (Plate LXXVIII, 423) greatly elongated to contain the elongated terebra of the adult within. According to Keilin (1913), the tegumentary glands of this larva are a provision against drought, which is the great source of danger to organisms living in this habitat.

Trentepohlia (*Paramongoma*) *leucoxena* (Alex.)

1915 *Mongoma leucoxena* Alex. Ent. News, vol. 26, p. 29–30.

Trentepohlia leucoxena was reared by Knab in Mexico, from larvae found living in bromeliaceous plants quite as in the preceding species.

Genus **Teucholabis** Osten Sacken (Gr. *weapons* + *forceps*)

1859 *Teucholabis* O. S. Proc. Acad. Nat. Sci. Phila., p. 222.

Larva.— Form elongate, slender, terete. Body practically destitute of pubescence and setae. Spiracular disk surrounded by three very broad lobes, a flattened ventral lobe and two shorter lateral lobes at the base of which are the small black spiracles. Gills four, bluntly rounded and developed for propulsion. Head capsule of four elongate, slender rods or plates, interno-lateral pair forked at about midlength. Mandible rather small, with about three blunt lateral teeth. Antenna elongate, two-segmented.

Pupa.— Cephalic crest setiferous. Pronotal breathing horns short, blunt, closely applied to thorax. Mesonotum precipitous, at crest with two powerful hooks and smaller serrated plates near shoulder. Wing sheaths reaching end of second abdominal segment. Leg sheaths reaching end of fourth abdominal segment, middle tarsi the shortest. Abdomen with a transverse row of setae before ends of segments.

Teucholabis is a rather extensive genus of small crane-flies (including more than fifty described species) which find their center of distribution in the Tropics of the New World. A few species occur in Africa and the Oriental region. The genotype, *Teucholabis complexa*, is the only species that has been reared (Johnson, 1900). Johnson's material was kindly sent to the writer for study, and furnishes the basis for the following descriptions.

Teucholabis complexa O. S.

1859 *Teucholabis complexa* O. S. Proc. Acad. Nat. Sci. Phila., p. 223.

Larvae of *Teucholabis complexa* were found by Johnson in considerable numbers beneath the bark of a decayed oak below Avalon, New Jersey, on June 8, 1899. They commenced pupating about the 13th, the imagines continuing to emerge from the 22d to the 27th. This gives a pupal duration of not more than nine days.

Larva.— Length, 9 mm.
Diameter, 0.55–0.6 mm.

Coloration pale yellowish white, spiracles conspicuously darker.

Form long and slender, body terete, tapering abruptly to the small prothoracic segment (Plate LXXIX, 424). Sutures between segments indistinct. Body practically destitute of pubescence and setae. Spiracular disk (Plate LXXIX, 427) with a broad, flattened, ventral lobe, which is very bluntly rounded to subtruncate at apex, and two very short, blunt, lateral lobes, at the base of which are the spiracles; spiracular disk without distinct markings. Spiracles small; middle piece black, ring pale horn-color; spiracles rather widely separated, the distance between them about equal to the long diameter of one. Anal gills (Plate LXXIX, 428) represented by four blunt, rounded lobes, which are apparently developed for propulsion rather than for a respiratory function.

Head not easily distinguishable in material available for study. Head capsule consisting of four long, slender, rodlike plates, the internal lateral pair forked at about midlength, so that capsule ends in six rods. Epipharynx with numerous small spines. Antenna (Plate LXXIX, 426) two-segmented, basal segment elongate-cylindrical, apical segment small, ovate. Mandible (Plate LXXIX, 425) rather small, apical point inconspicuous, with about three similar lateral teeth below it. Lobes of the maxilla blunt, stout, hairy, not extending far beyond tip of mandible.

Pupa.— Length, 6.5–6.6 mm.
Width, d.-s., 1–1.1 mm.
Depth, d.-v., 1.2 mm.

Coloration pale; head, thorax, and sheaths of appendages darker; eyes black.

Form slender, narrowed behind. Between antennal bases a prominent, two-parted crest each lobe somewhat truncated behind and bearing a single stout seta. Front above eyes

slightly raised, two narrow lines on front, meeting below at a very acute angle. Eyes large in male, smaller in female, the front correspondingly narrowed or broadened. Labrum short, subtriangular. Sheaths of labial lobes small, suboval, separated by tip of labrum. Sheaths of maxillary palpi short, stout, straight. Antennal sheaths moderately long, extending to just beyond wing base; basal segments prominent, indicated on sheath as prominent elevations. Pronotal breathing horns short, blunt, anterior face closely applied to pronotum, outer face free; at base a small rounded knob. Thorax very deep, precipitous, at crest (Plate LXXIX, 429) armed with two strong curved hooks, one on either side of median line; on shoulder laterad of these hooks, two prominent flattened plates whose margins are minutely serrated, the dorsal, or outer, plate being the larger and terminating in a large curved hook. Wing sheaths moderately broad, ending just before tip of second abdominal segment. Leg sheaths (Plate LXXIX, 430) long and slender, outer pair much the longest, ending about opposite tip of fourth abdominal segment, middle pair the shortest. Mesonotum with two strong setae.

Abdominal segments divided into two annuli by an indistinct suture, anterior ring narrow; anterior ring with a strong seta on pleural region; posterior ring with strong setae on dorsum and sternum near caudal margin; three other setae on pleural region, two at about midlength of segment, the third near base and more dorsal in position. Male cauda (Plate LXXIX, 431) suddenly narrowed, terminating in two blunt ventral lobes and two acutely pointed dorsal lobes bent strongly dorsad at their tips and bearing a short seta in notch on inner face before apex; near base of cauda, on dorsum, a broad transverse swelling terminating in two widely separated, slender tubercles, immediately cephalad and laterad of which is a long seta; three strong setae on either side near base of cauda; posterior margin of segment 7 with two powerful, decussate setae on dorsum, and between them two small setae; another powerful seta near pleural region, and just inside still another smaller seta.

Nepionotype.— Avalon, New Jersey, June 8, 1899.
Neanotype.— With type, June 14, 1899.
Paratypes.— One larva and one pupa.

Genus **Cladura** Osten Sacken (Gr. *branch* + *tail*)

1859 *Cladura* O. S. Proc. Acad. Nat. Sci. Phila., p. 229.

The genus Cladura includes six known species — two from eastern North America, one from western North America, and three from Japan. The small *Cladura delicatula* Alex., of the mountainous regions of the northeastern United States, differs from the genotype, *C. flavoferruginea* O. S., in several important respects and it is necessary to erect a new group to receive it. This group may, for the present at least, be considered as a subgenus of Cladura, and the name *Neocladura* (Gr. *new* + *Cladura*) is proposed. Moreover, the genera Crypteria Bergr. and Pterochionea Alex. are closely related to Cladura, and the entire group are almost certainly the direct forbears of the subapterous genus Chionea Dalman. Neocladura

curiously combines the structural characters of Cladura, Pterochionea, and Crypteria. In the long basal fusion-segment of the antennal flagellum and in the wing venation, it agrees with Pterochionea and, to a somewhat lesser degree, with Cladura. In the structure of the male hypopygium, which has two slender pleural appendages, it departs widely from the type of typical Cladura, Chionea, and Pterochionea, and agrees better with Crypteria, as well as with Conosia v. d. W. and Lecteria O. S. Because of this combination of characters, Neocladura must be separated in some manner from Cladura in the strict sense. It must be borne in mind, however, that the conspicuous difference in the structure of the male hypopygium probably has a phylogenetic significance, and the two flies may not be so closely united as this arrangement would indicate.

The habits of the adult flies of Cladura and Neocladura are generally similar. Both species fly in late summer and in the autumn. They often occur on dry, wooded hillsides remote from streams and other bodies of water. The habits of the adult flies of *Cladura flavoferruginea* have been discussed by the writer in an earlier paper (Alexander, 1910:250, as *C. indivisa*). His observations, made near Gloversville, New York, on September 22, 1909, are as follows:

> I went to Simmon's Woods, southeast of Gloversville, New York, this afternoon, and was very agreeably surprised at the occurrence, in large numbers, of this usually uncommon insect. Near the entrance of the woods, where Simmon's Brook emerges, the insects were found in numbers. At each step they flew out of the bushes to others farther away. They are wary insects, and when sitting on the upper side of a leaf, slip over the edge and hang inverted from the lower side when alarmed by an observer. They present a very characteristic attitude, sitting on the leaf of a tree, with their wings folded flat over the abdomen, and the six long legs stretched out over the leaf. A few were taken in copulation; these were all hanging on the under side of a leaf. Their habit of clinging to the under surface of a leaf is quite remarkable and I found several by looking for them there.
>
> There were hundreds of specimens in the low bushes of the woods, usually on the broad leaves of deciduous trees at a height of two or three feet. Sometimes they would alight on hemlock, and, occasionally, in ferns near the ground. It was the only tipulid observed here to-day.

The eggs of *C. delicatula* have been taken from gravid females. They are comparatively few in number, but because of their unusual size they almost fill the entire abdominal cavity of the fly. These large eggs are elongate-ovate in shape.

Cladura flavoferruginea O. S.

1859 *Cladura flavoferruginea* O. S. Proc. Acad. Nat. Sci. Phila., pl. 4, fig. 34.
1861 *Cladura indivisa* O. S. Proc. Acad. Nat. Sci. Phila., p. 291.

The immature stages of *Cladura flavoferruginea* were discovered while this paper was in press. A brief account of the larvae and pupae are given here in order to complete the data.

The larvae were found in Augurville Woods near Urbana, Illinois. They occurred in soil which was baked hard and dry and which supported scarcely any other insect life. Associated with the larvae when first discovered were larvae of a scarabaeid, *Xyloryctes satyrus*; a tenebrionid, *Meracantha contracta*; a few dipterous larvae of the genera Sciara and Psilocephala; millepedes of the genus Spirobolus; and a few less common forms of animal life. A layer of dead leaves and other decaying vegetable matter covered the surface, but this had not prevented an almost complete drying out of the soil to a depth varying from six inches to more than a foot. The only other tipulid larvae characteristic of such dry soil are species of Dicranoptycha (page 828).

The most conspicuous features of the pupa are its exceedingly small size as compared with the adult fly that emerges from it, and the entire lack of protuberant pronotal breathing horns.

Larva.— Length, 10–10.5 mm.
Diameter, 1.2 mm.

Coloration light yellow thruout.

Form comparatively short and stout. Integument provided with a delicate appressed pubescence; no distinct setae. Basal annulus of abdominal segments 2 to 7 with a transverse area of microscopic points arranged in long transverse rows; last ventral segment with a flattened lobe covered with short setae, evidently an organ for shoving. Spiracular disk entirely without lobes, the spiracles being located on the exposed dorso-caudal surface of the last abdominal segment. Head capsule relatively compact; frontal plate broad, only slightly narrowed behind. Labrum quadrate, with conspicuous oval lateral arms. Antenna two-segmented, terminal segment elongate-oval. Mandibles of a herbivorous type, with an apical point and two incomplete rows of teeth on inner, or cutting, face. Mental bars widely separated, each bar provided with two acute teeth at its proximal end.

Pupa.— Length, 6.7 mm.
Width, 1.4 mm.
Depth, 1.4 mm.

Coloration pale yellow; head, thorax, and appendages darkening in age.

Cephalic crest gibbous, entire or feebly bifid, armed on either side with a single powerful bristle; two bristles on vertex and two on front; labrum with a pair of small bristles at each cephalic lateral angle. Labial lobes subquadrate, weakly separated by apex of labral sheath. Palpal sheaths short and stout, straight. Lateral margin of eye produced laterad into a digitiform lobe. Antennal sheaths extending to opposite one-third length of wing sheaths. Pronotal breathing pores entirely sessile. Pronotum and mesonotum armed with

conspicuous bristles. Wing sheaths ending opposite base of third abdominal segment. Leg sheaths unusually long, ending opposite base of sixth abdominal segment; hind legs the longest, middle legs the shortest. Abdominal tergites with ten strong bristles, eight being arranged in a single transverse row along posterior margin; abdominal pleurites with four strong bristles, one on each anterior ring, two near caudal margin of posterior ring, one ventrad of spiracle, the last-named rudimentary, located on segments 2 to 7; sternites unarmed with bristles.

Genus **Chionea** Dalman (Gr. *snow*)

1816 *Chionea* Dalm. K. Vet. Akad. Handl., vol. 1, p. 102.
1912 *Sphæconophilus* Beck. Ann. Soc. Ent. Belgique, vol. 56, p. 142.

Chionea is a small genus of nearly apterous crane-flies, found thruout the North Temperate Zone. All of the known species (about eight) have the wings reduced to mere vestiges, this being the only genus of considerable size in which all the species show this condition. The South African genus Platylimnobia Alex., which shows a somewhat similar condition of wing atrophy, is probably not very closely allied to Chionea.

The adult flies of Chionea are most often found walking awkwardly over the snow in the late fall or early spring or during warm days in winter. A few instances, however, have been recorded in which specimens were found with the temperature below freezing. At other seasons of the year they may be found among fallen leaves, under moss and stones, in the nests of small mammals as Arvicola (Schmitz, 1914), or in deserted subterranean wasps' nests (Schmitz, 1916, and Becker, 1912). Interesting accounts of the habits of the adult flies of the commonest local species, *Chionea valga* Harris, are supplied by Ainslie (1906), Johnson (1907), Washburn (1907), and others. Lugger (1896) gives the following interesting account of the habits of the same species:

> As a general rule the wingless flies are found only early in the morning, though in one case a female was discovered crawling over the snow in the evening. . . . A few winters ago the writer discovered a female moving slowly over the snow and by searching he soon detected a male. Putting both together under an inverted glass the snow-flies immediately mated, notwithstanding it was several degrees below the freezing point. Soon afterward the female found a crack in the glassy surface of the frozen snow, and forcing herself into it slowly disappeared from view. Penetrating for some depth into the snow she deposited a number of elongated eggs, which, however, did not hatch. Most females found seemed to have the eggs already fully matured and only lacked to be fertilized.

Frauenfeld (Brauer, Egger, and Frauenfeld, 1854:616) believed that the eggs are deposited in snow, since they are often laid in January or February. He thought the slimy substance secreted by the small lateral

vesicles of the *receptaculum seminis* of the female acts as a covering to protect the eggs from wet and cold. It seems probable, however, that the flies enter some crevice in the snow around the base of trees or shrubs and reach solid earth, at least in some cases. Many authors have held the flies to be nocturnal in their habits. Recently, Marchand (1917) has furnished some interesting notes on an alpine Chionea, presumably *C. alpina* Bezzi. His observations and experiments showed him that Chionea was perfectly adapted to life on the snow, being attracted to this medium by its bright light and white color, the contact of the cold surface on the feet resulting in a direct stimulus thru the claws. The insects drink water by pressing their proboscides against the snow. Marchand considers the principal reason for these activities' being held on the snow to be for the purpose of mating, since the insects can cover considerable distances over the level surfaces and are much more visible to one another at this time. The copulation of this crane-fly has been fully described by Mik (Osten Sacken, 1887:196) as follows:

> The upper valves of the ovipositor prevent the male from getting on the back of the female; it lies on its own back, in the direction of the longitudinal axis of the body of the female; when the latter is walking it drags the male, who raises himself on his hind legs to an almost perpendicular position; this serves to explain the unusual incrassation of these legs.

The genotype, *C. araneoides* Dalm., is the only species whose immature stages have been described.

Chionea araneoides Dalm.

1816 *Chionea araneoides* Dalm. K. Vet. Akad. Handl., vol. 1, p. 104.

The present knowledge of the life history of *Chionea araneoides* is due almost entirely to the work of Brauer, Egger, and Frauenfeld (1854). In February these investigators brought living adults, taken in copula, into an unheated room and placed them with their natural surroundings, such as rich, damp, humous earth, rotten grape leaves, and similar substances, in glass containers. After a time a great number of small, elongated eggs of a hyaline appearance were noted, laid at random, some being deposited on the walls of the container, where they adhered but soon shrunk and appeared dried out. Unfortunately the duration of the egg stage was not ascertained. Some weeks later the young larvae were found in the soil. They were of a cylindrical form, very pale yellow in color and not especially active. They were associated with numerous

larvae of *Sciara longipes* Meig. Toward the end of May only a few larvae were left, and these appeared fully grown but were not carried over into the pupal condition, which is still unknown.

Larva.— Length when fully grown, 7.4 mm.

Color light reddish yellow, contents of alimentary tract showing thru body. Body terete (Plate LXXXII, 443), consisting of twelve segments, there being, besides the head, three thoracic and nine abdominal segments; last segment wedge-shaped (Plate LXXXII, 446 and 447), obliquely truncated so that the surface slopes from behind upward. Two spiracles on this oblique surface, with a paler brown, pincer-shaped mark between. Mouth parts powerfully constructed. Mandible (Plate LXXXII, 444), produced into a long apical point; near midlength on inner edge of mandible a deep incision, distad of this about five teeth, basad of it three teeth. Labrum quadrangular, with two lateral points on anterior part. Mentum projecting outward as a cuticular rounded lobe. (Brauer shows two other appendages which are toothed on the outer face [Plate LXXXII, 445, of this paper]; these probably represent part of the mentum, but from Brauer's figures they would appear to lie above the labrum.)

Subtribe **Elephantomyaria**

Genus **Elephantomyia** Osten Sacken (Gr. *elephant* + *fly*)

1859 *Elephantomyia* O. S. Proc. Acad. Nat. Sci. Phila., p. 220.

Larva.— Form terete. Segments of body just before sutures with transverse rows of stiff hairs; abdominal segments 5 to 8 on ventral surface with a mouthlike depression surrounded by long, stiff hairs. Spiracular disk surrounded by four lobes, ventral pair the longest, each of the latter bearing at its tip a single very long bristle. Spiracles moderately large, located at base of lateral lobes. Head capsule very long and narrow, the four plates very elongated. Mandible very small. Maxillary palpi short. Esophageal region surrounded by chitinized plates which are conspicuously obliquely ridged. Body of larva covered with numerous long, appressed hairs, producing a satiny appearance. Coloration saturated golden yellow.

Pupa.— Form slender. A small crest on vertex above eyes. Eyes very large, globular, narrowly separated on frontal and vertical regions. Rostral sheath very elongated; palpi recurved against it. Antennal sheaths lying across eye. Head and thorax with setiferous tubercles. Abdomen with rudimentary lateral spiracles.

Elephantomyia is a small genus of crane-flies including about a dozen described living species. These are found in widely separated regions of the world, there being about four in the East Indies, five in Africa, and two in North America, one of which has been recorded also from Europe. The genus is found fossil in the Baltic amber. The adult flies are remarkable for their very elongated rostra, and undoubtedly they feed on the nectar of tubular flowers as in the related genus Toxor-

hina. No records are available, however, to indicate what species of plants are thus frequented. The larvae live in decaying wood. The only species whose immature stages are known is the genotype, *Elephantomyia westwoodi.* The literature on the immature stages of this group of flies is very limited, the only record being the unknown Limnobiine No. 1 of Malloch (1915–17 b:235–236), who gives a good description of the larva. The pupa is here described and figured for the first time.

Elephantomyia westwoodi O. S.

1869 *Elephantomyia westwoodi* O. S. Mon. Dipt. N. Amer., part 4, p. 109.

Elephantomyia westwoodi is a rather common fly in eastern North America. The adults are usually found in cool, shaded woods and may be swept from vegetation in these localities. The larva lives in decaying wood, as is shown by the three records available to the writer.

The larvae were found by Shannon in a very wet, rotten, willow log lying near the tidal flat above the brewery at Rosslyn, Virginia, on May 21, 1913. About eight larvae were found, well scattered thru the log. They were very active in their movements and were very beautiful, in life being of a deep golden yellow color. These larvae were placed in rearing, and adults issued on May 27 and 29 and June 5 and 7, indicating a pupal duration of a week or slightly less. Larvae were found in this log also on November 23, 1912, and at that time they were almost grown, being about one-half inch in length. This shows that the species spends the winter as almost fully grown larvae.

Johnson found these larvae near Edge Hill, Pennsylvania, on June 25, 1899, and on May 25, 1905, in a log, just beneath the bark. Larvae and pupae obtained by him were in the material studied in the preparation of this paper.

Malloch found a single larva of this species in a much decayed log at White Heath, Illinois, on April 30, 1916 (Malloch, 1915–17 b:236).

Larva.— Length, 10–13.4 mm.
Diameter, 1.2–1.3 mm.

Coloration of body, a deep saturated golden yellow thruout.

Body moderately elongated, terete, relatively slender, tapering gradually toward either end but more noticeably and abruptly toward anterior end (Plate LXXX, 432); the three thoracic segments gradually increasing in size from the prothoracic backward. Abdominal segments 1 and 2 short, the third to the fifth the longest, remaining segments gradually shorter. Sur-

face of body densely covered with long, satiny, appressed hairs; thoracic and abdominal segments with a dorsal and a ventral transverse ridge of short, stiff hairs just before caudal margins of segments, these being longest on lateral parts of ridge; dorsal segments 6 and 7 with incomplete transverse rows at about midlength; on ventral surface of abdominal segments 1 to 3, near base, two transverse rows of tiny spines with a depressed area between; segment 4 without this distinct double ridge; segments 5 to 7 with a very conspicuous mouthlike depression at base of each, with a liplike margin on either side, the anterior margin narrow with stiff hairs, the posterior margin swollen and densely set with tiny spines; on segment 8 the transverse mouth lying near end of segment, its anterior lip with a dense fringe of long hairs directed backward. Spiracular disk (Plate LXXX, 434) surrounded by four lobes; lateral lobes the shortest, blunt at tips, inner face of each lobe slightly expanded at tip, a few short silky hairs on outer face of lobe, inner face slightly chitinized; ventral lobes longer, broad, tapering gradually to obtuse tips, notch between lobes deep, V-shaped, a narrow fringe of short, dense, golden, recurved hairs along outer face; at tip of each ventral lobe a single long, powerful bristle. Spiracular disk unmarked. Spiracles large, very widely separated, situated at base of lateral lobes.

Head capsule (Plate LXXX, 433) very small and narrow, the plates, four in number, being greatly elongated. (The exact details are difficult to see in the material available for study.) Labrum broad, anterior margin evenly rounded, with a few long hairs. Epipharyngeal region provided with long setae directed backward. Mandible very small, base narrowed, tip produced into an acute point with smaller teeth at about midlength. Mental region feebly chitinized. Hypopharynx semicircular, rounded, anterior margin delicately grooved. Esophageal region elongated, inclosed by chitinized plates provided with parallel ridges running outward on one side and inward on opposite face, upon focusing producing a latticed appearance. Maxilla densely hairy. Antenna two-segmented, conspicuous; basal segment short, apical segment larger, suboval. Sides of capsule on swelling behind the maxilla with a brush of very long hairs. Plates of capsule elongated, expanded and chitinized at tips and along margins; ventral plate near esophageal region with setae.

Pupa.— Length, 8.4 mm.
Width, d.-s., 1.1 mm.
Depth, d.-v., 1.3 mm.

Coloration light yellowish brown; abdomen darker; thoracic dorsum, sheaths of legs, and ovipositor more yellowish. (In younger pupae the coloration is more uniformly pale.)

Form slender, body narrow. Eyes very large, rounded (Plate LXXXI, 441). Antennal sheaths lying directly across face of eye. Vertex with a small but prominent crest lying transversely above eyes; cephalad of this crest and just proximad of the antennal bases, a setiferous tubercle. Front between eyes moderately broad, produced caudad into the very elongate rostral sheath, which is transversely wrinkled. Sheaths of maxillary palpi recurved, lying alongside rostrum. Sheaths of labium tiny, bilobed, lying at tip of rostrum. Two long setae on front between eyes. Eyes very large, narrowly separated on dorsum of head, the hinder part sunken under pronotum. Two conspicuous black tubercles behind antennal bases, each bearing a long, stout seta. Pronotal breathing horns (Plate LXXX, 435) small,

short, clavate, yellow, constricted at bases, which are blackened; a prominent seta just above each breathing horn; two setae on each side of pronotum beneath eye. Mesonotal prescutum strongly convex, with six strong setae on each side, one just cephalad of base of wing, another at joint of wing, and two semitransverse groups in front of and behind level of wing base. Wing sheaths short, ending some distance beyond tips of hind tibiae and just beyond base of third abdominal segment. Leg sheaths (Plate LXXXI, 442) with fore femora strongly swollen, lying alongside rostral sheath; tips of middle tibiae ending just beyond tips of fore tibiae; legs very long, ending just before tip of fifth abdominal segment.

Abdominal segments densely and microscopically punctulate. Segments 2 to 7 with two narrow basal rings and a broad posterior ring. Setae of dorsal abdominal segments (Plate LXXX, 437) on the posterior ring consisting of a caudal series of two strong outer setae and two smaller inner ones, the outer one of the inner series close to the proximal one of the outer series; lateral series of setae powerful; basal series in alinement with anterior lateral seta, consisting of two powerful outer setae and a delicate inner one; pleural segments with a rudimentary spiracle on segments 2 to 7, each spiracle with a stout seta above it; setae of ventral segments (Plate LXXX, 436) with two strong bristles on each side near posterior lateral margin, the outermost with a tiny seta above it; a single basal seta located on a level with vestigial spiracles. Female cauda (Plate LXXX, 439) with sternum of eighth segment having two sharp, curved, widely separated spines, and just laterad of these a stout seta; pleural region with another seta on same level; sternal valves of ovipositor only a little shorter than tergal valves; dorsum of segment 8 with two long teeth, above which are two slender, divergent tubercles; tergal valves broad basally, narrowed suddenly at tip, on either side with a small, subapical seta. Male cauda (Plate LXXX, 438 and 440) with eighth sternite having a strong median tubercle that is two-toothed; laterad of this a strong chitinized tooth bearing a powerful seta on outer face; a similar strong lateral seta; eighth tergite with four strong tubercles arranged to form a square; ninth sternite blunt, each lobe ending in two small tubercles; ninth tergite ending in two divergent lobes bearing at tip a large and a small seta and on dorsal face at about midlength another strong seta.

Nepionotype.— Rosslyn, Virginia, May 21, 1913.
Neanotype.— Edge Hill, Pennsylvania, May 25, 1905.
Paratypes.— Larvae with type larva (two) and with type pupa (two).

Genus **Toxorhina** Loew (Gr. *bow* + *nose*)

1835 *Limnobiorhynchus* Westw. Ann. Soc. Ent. France, p. 683 (spurious name).
1851 *Toxorhina* Loew. Linnaea Entomol., vol. 5, p. 400.
1869 *Toxorrhina* O. S. Mon. Dipt. N. Amer., part 4, p. 109–114.
1910 *Neoceratocheilus* Wesché. Journ. Linn. Soc., Zool., vol. 30, p. 358.

Toxorhina is a small genus including about nine described species, almost all of which are from the New World. Two species occur in Africa and one in India. *Toxorhina madagascariensis* Meun. is described from African copal (Pleistocene). Nothing has been published concerning the immature stages of any member of this genus.

Toxorhina muliebris (O. S.)

1865 *Toxorrhina muliebris* O. S. Proc. Ent. Soc. Phila., p. 233.

Toxorhina muliebris is the commonest species of the genus in the United States, with a rather wide range thruout the Northeastern States. The adult flies suck nectar from various flowers, such as the following: Rhamnaceae, *Ceanothus americanus* Linn. (Banks); Ericaceae, *Clethra alnifolia* Linn. (McAtee); Apocynaceae, *Apocynum medium* Greene (McAtee); Compositae, *Solidago canadensis* Linn. (Knab).

The immature stages are unknown, but from Mrs. Tothill's tent-trap observations they are presumably spent in mud, since adult flies were found in her traps set over wet, sedgy spots near Ithaca, New York. It may be, however, that the insects live in fragments of decaying wood which might be buried in this mud, since such a habitat conforms more closely to that of Elephantomyia, which is apparently closely related to Toxorhina.

Eriopterine No. 1

A very curious larva, which has not been reared, has been found in various places near Ithaca during the past few years. It is a small, pale larva, very delicate and almost diaphanous in appearance, at the posterior end with five flattened black plates with serrated margins, and with its thoracic segments capable of considerable lateral extension. The larva is undoubtedly an eriopterine, but it introduces a type of spiracular disk that has not been found elsewhere in the tribe. The writer finds it difficult to believe that this curious larva can belong to any of the eriopterine genera discussed in this paper, and yet there are very few possibilities remaining; and one of these (Cryptolabis) does not occur in the habitat frequented by this larva. The genus Atarba, whose immature stages are still wholly unknown, is a possibility. Empeda, which the writer considers to be a subgenus of Erioptera, has not been reared and must also be considered as a possibility. If this is the larva of Empeda, the group at once assumes full generic rank as given it by Osten Sacken, but occupying an isolated position and no closer to Gonomyia than to Erioptera. The larvae of this species were found commonly on Bool's hillside, at Ithaca, where they occurred in association with numerous other crane-fly larvae discussed elsewhere (page 781). The

larva is described here in the hope that it will be reared and its identity ascertained.

Larva.— Length, 7–8.2 mm.
Diameter, 0.4–0.5 mm.

Coloration pale yellowish white; skin very delicate, almost diaphanous.

Body moderately elongated, terete; meso- and metathoracic segments (Plate LXXV, 404) and eighth abdominal segment capable of considerable expansion laterally, and, in death, usually greatly swollen; last segment of body narrowed, cylindrical, with a number of long setae, including a group of five near base of lateral lobes. A few scattered setae along abdominal segments. Spiracular disk (Plate LXXV, 405) surrounded by five equal elongate spatulate blades, these blades flattened, jet-black in color, margins finely toothed; paired lobes near base with a subhyaline median spot; margins of lobes (Plate LXXV, 406) with twenty-five to thirty hooks, recurved ones alternating with others laterally directed; when blades are closed, these margins hooking closely together; at ends of blades and sparsely scattered along margin, long, delicate setae; at apex of blades, two bristles; no spiracles found at base of lobes. Anal gills four, lateral pair elongated, telescopic, inner pair shorter.

Head capsule much as in other eriopterine genera, especially Ormosia and Gonomyia, dorsal plates slender, ventral bars a little longer. Labrum as in the tribe; epipharyngeal region with a large apical setiferous pad and two smaller pads nearer base. Mentum not formed of ventral bars of capsule as in Molophilus. Hypopharynx a semicircular cushion covered with long, dense setae, their tips a little recurved. Antenna with apical papilla very long for this tribe, about equal in length to basal segment, cylindrical, with tip rounded. Mandible moderately large, apical tooth not prominent, lateral teeth rather conspicuous, basal ones smaller but not so excessively reduced as in other members of the tribe; prostheca large.

(Described from larvae, Ithaca, New York, May 11, 1917. No. 29–1917.)

Tribe Styringomyiini

The Styringomyiini comprise a small group of very peculiar crane-flies with a tropicopolitan distribution. There is only the single genus, Styringomyia, with about twenty-five described species. Most of the species are from tropical Africa and Asia, tho a few range into Australia and the Hawaiian Islands, and one, *Styringomyia americana* Alex., is found in tropical South America.

Genus **Styringomyia** Loew (Gr. *a kind of tree-gum + fly*)

1845 *Styringomyia* Loew. Dipt. Beitr., vol. 1, p. 6. (Correctly *Syringomyia* — Bergroth *in litt.*)
1903 *Idiophlebia* Grünb. Zool. Anzeig., vol. 26, p. 524–528.
1912 *Pycnocrepis* Enderl. Zool. Jahrb., vol. 32, part 1, p. 65.
1917 *Mesomyites* Ckll. Proc. U. S. Nat. Mus., vol. 52, p. 377.

The history of the genus Styringomyia is remarkable. It was erected by Loew in 1845, being based on the fossil species *Styringomyia venusta* Loew, from African copal. Many years later it was found to be still living in the Tropics of both hemispheres. The earliest fossil records pertain to the Oligocene of northern Europe (page 765).

The adult flies have such a curious structure that it seems best to remove them from the former tribe Antochini, where they have long been placed. Concerning the first living species to be described, the Hawaiian *S. didyma* Grimsh., Perkins (1913: clxxxii) says:

It sometimes swarms at night around the electric lights, sitting quietly on the walls and ceilings, with the body pressed closely to the surface, and the front and middle legs extended straight forward in front of the head in a characteristic manner.

Annandale has made similar observations on the resting positions of *S. ceylonica* Edw., taken in India. He says (cited by Edwards, 1914–15: 207): "This species rests on walls with the two anterior pairs of legs stretched out straight in front and the posterior pair behind, resembling a stray piece of cobweb." Jacobson has recorded much the same for *S. jacobsoni* Edw. (De Meijere, 1911: 41–42, as *S. didyma*) in Java. The flies are attracted to lamps and are almost always to be found in copulation, the head of one directed away from the other; while thus engaged, sometimes one, sometimes the other, will run forward for a short distance, producing a peculiar appearance. Munro (*in litt.*) reports that the habits of *S. vittata* Edw. as observed in eastern Transvaal in late April, 1920, are very similar. He writes: "Two specimens taken 'in cop.' Settled on under side of a twig, heads in opposite directions, front legs of each stretched out in front along twig, wings laid flat along abdomen."

Styringomyia didyma Grimsh.

1901 *Styringomyia didyma* Grimsh. Fauna Hawaiiensis, p. 10.

In *Fauna Hawaiiensis*, Perkins (1913: clxxxii) mentions the breeding of *Styringomyia didyma* by F. W. Terry. Before the reference could be investigated by the writer, Mr. Terry died. The following letters from O. H. Swezey in regard to the matter were then received.

In response to a letter sent on February 21, 1915, Mr. Swezey replied on March 26 that "no information on the rearing of the species is available in Mr. Terry's notes."

In a letter dated April 10 of the same year, however, the following notes were enclosed:

About forty-five eggs deposited in tube December 5, 1910. Chorion jet black, shining and thick, resisting dryness; 0.3 mm. by 0.15 mm., very finely parallel-striate.

One hatched December 10. The batch was placed with rotten apples and cow manure, hatching December 15. Larva long, head small, mandibles distinct and well chitinized.

An adult male emerged about January 21, 1911.

Mr. Swezey, thru whose kindness the above notes are available, adds: "You see from the notes of Terry's that he did not breed *Styringomyia didyma* in its natural habitat. That is yet unknown, I guess."

The striking feature of this life history is its brevity, the entire egg, larval, and pupal stages being passed in about a month and a half. The writer knows of no other crane-flies in which this is equaled, its nearest approach presumably being in the smaller Eriopterini.

SUBFAMILY **Cylindrotominae**

The subfamily Cylindrotominae constitutes a small, isolated group of crane-flies, with twenty described species arranged in seven recent genera. All the species are Holarctic in their distribution with the exception of five species of the Oriental genera Stibadocera Enderl., Stibadocerella Brun., and Agastomyia de Meij. The group is a decadent one, having been much better developed in the early and middle Tertiaries than at present (page 764).

The adult flies are sluggish in their habits, occurring on vegetation in cool, shaded spots. The species of Cylindrotoma are brightly colored, yellow and black, but the other forms are somber in appearance and black or dark in color, the body being in some cases highly polished or metallic. The immature stages of the Cylindrotominae differ from those of all other Tipulidae, so far as is known to the writer, in being spent on various bryophytic and spermatophytic plants, on the leaves of which the larvae feed. The larvae are usually bright green in color and suggest a caterpillar in their general form. Most of them simulate their host plants to an astonishing degree. The immature stages of Cylindrotoma and Liogma are terrestrial, while those of Triogma and Phalacrocera are aquatic or nearly so.

The genera of the subfamily Cylindrotominae may be separated as follows:

Larvae

1. Body appendages very long and filiform; aquatic .... *Phalacrocera* Schin. (p. 961)
   Body appendages short, leaflike or tuberculate 2
2. Dorsal appendages all simple, on the terminal abdominal segments in a single row; terrestrial on spermatophytic plants...................... *Cylindrotoma* Macq. (p. 966)
   Dorsal appendages with teeth on anterior convex side 3
3. Some of the dorsal appendages with three or four teeth on anterior face; aquatic on mosses.. *Triogma* Schin. (p. 973)
   Dorsal appendages with one (*L. nodicornis*) or two (*L. glabrata*) teeth.
   Liogma O. S. (p. 969)

Pupae

1. Basal abdominal tergites without spines 2
   Basal abdominal tergites with acute spines......................................3
2. Mesonotum unarmed; segments 6 and 8 each with two powerful dorsal hooks; segment 7 with a pair of strong ventral spines; pronotal breathing horns elongate, directed backward.. *Phalacrocera* Schin. (p. 961)
   Mesonotum with two flattened erect lobes; segments 6, 7, and 8 naked; pronotal breathing horns small, directed slightly forward.................. *Cylindrotoma* Macq. (p. 966)
3. Abdominal spines branched .... *Liogma* (*glabrata*) (p. 969)
   Triogma (*trisulcata*) (p. 974)
   Abdominal spines not branched........................ *Liogma* (*nodicornis*) (p. 971)

The most important literature on the Cylindrotominae is as follows:

General account of subfamily. Osten Sacken, 1897; Alexander, 1914:105–106; Malloch, 1915–17 b:210–211; Lenz, 1920 b:113–115.

Phalacrocera replicata	Larva, pupa, general	De Geer, 1773; 1776:135–141, 351.
Phalacrocera replicata	Larva	Grube, 1868.
Phalacrocera replicata	Larva	Engel, 1884.
Phalacrocera replicata	General	Giard, 1895 b.
Phalacrocera replicata	Larva, general	Bengtsson, 1897. (Morphology of larva.)
Phalacrocera replicata	Larva, pupa, general	Miall and Shelford, 1897. (Morphology of larva and pupa.)
Phalacrocera replicata	Larva	Bengtsson, 1899. (Morphology of heart.)
Phalacrocera replicata	Larva	Holmgren, 1908. (Morphology of head.)
Phalacrocera replicata	Larva, pupa	Grünberg, 1910:32–35.
Phalacrocera replicata	Larva, pupa, general	Wesenberg-Lund, 1915:343–347.
Phalacrocera replicata	Larva, pupa, general	Lenz, 1920 b:127–129.
Cylindrotoma distinctissima	Larva, general	Schellenberg, 1803:22–23.
Cylindrotoma distinctissima	Larva, pupa, general	Boie, 1838:234.
Cylindrotoma distinctissima	Larva, pupa, general	Zeller, 1842.
Cylindrotoma distinctissima	General	Schiner, 1864:563.
Cylindrotoma distinctissima	Larva, pupa, general	Kaltenbach, 1874:7.
Cylindrotoma distinctissima	Larva	Wesenberg-Lund, 1915:335 (as Triogma).
Cylindrotoma distinctissima	Larva, pupa, general	Lenz, 1920 b:115–117.
Cylindrotoma splendens	Larva, pupa, general	Cameron, 1918.
Liogma glabrata	Larva, general	De Rossi, 1876.
Liogma glabrata	General	Osten Sacken, 1878 a.

Liogma glabrata..............	Larva, pupa, general...	Müggenberg, 1901.
Liogma glabrata..............	Larva, general........	De Rossi, 1902.
Liogma glabrata..............	General..............	Alexander, 1914:106–107.
Liogma glabrata..............	Larva, pupa, general...	Lenz, 1920 b:117–121.
Liogma nodicornis............	Larva, pupa, general...	Alexander, 1914:107–115.
Triogma trisulcata............	Larva, general........	Steinmann, 1907–08.
Triogma trisulcata...........	Larva, pupa, general..	Müller, 1908–09.
Triogma trisulcata...........	Larva, general........	Wesenberg-Lund, 1915:347–348 (as *Liogma glabrata*).
Triogma trisulcata...........	Larva, pupa, general...	Lenz, 1920 b:121–127.

Genus **Phalacrocera** Schiner (Gr. *bald* + *horn*)

1863 *Phalacrocera* Schin. Wien. Ent. Monatschr., vol. 7, p. 224.

Larva.— Body covered with numerous elongate, trachea-bearing filaments, the posterior pair on dorsal segments deeply forked, the others simple. Spiracular disk with dorsal pair of lobes formed by rudimentary posterior branch of branched filaments of eighth abdominal segment. Head capsule compact. Mentum with about fifteen teeth.

Pupa.— Cephalic crest low, not setiferous. Pronotal breathing horns long, almost straight. Dorsal abdominal segments with tubercles, those of sixth and eighth segments enlarged into spinous hooks; two pointed tubercles on seventh sternite.

Phalacrocera is a small genus (four species) of medium-sized to large, dull-colored flies, of which the genotype, *Phalacrocera replicata*, is European, *P. mikado* Alex. is Japanese, and the two remaining species are North American.

The adult flies of the American species are not common, the best-known, *P. tipulina* O. S., being most frequently found in or near sphagnum bogs in mountainous localities. Needham (1908 a:209) found the wings of an individual of this species in the pitcher plant, *Sarracenia purpurea* Linn., in the Adirondack Mountains, together with the wings of four specimens of *Elephantomyia westwoodi* and numerous other insects. Most of the specimens that have been found by the writer were taken in close proximity to bogs.

The immature stages of *Phalacrocera replicata* have long been known, having been described by De Geer and other early workers on insect biology. More recently the life history, anatomy, and morphology have been discussed in commendable detail by several other writers (page 960). Both the larvae and the pupae are aquatic, living among submerged plants in quiet, but non-stagnant, water.

The immature stages of *P. tipulina* are very much to be desired, as the adult shows some features in its organization not found in the other species of the genus.[6]

[6] The larva of this species was discovered by J. Speed Rogers in 1920.

Bengtsson (1897) erected for this genus the group Erucaeformia, which he considered as the primitive form from which the Nematocera and the Brachycera have been derived. This group, of course, has no standing whatsoever.

Phalacrocera replicata (Linn.)

1761 *Tipula replicata* Linn. Fauna Suecica, 2d ed., p. 500–502.
1863 *Phalacrocera replicata* Schin. Wien. Ent. Monatschr., vol. 7, p. 224.

The larvae and the pupae of *Phalacrocera replicata* have been discussed in such detail by Miall and Shelford, by Bengtsson, by Holmgren, and by Wesenberg-Lund, that they are considered here only in general terms. The habits of the immature stages have been discussed by many writers since the time of De Geer. They are oftentimes rather numerous among aquatic plants such as *Ranunculus fluitans* Lam., *Fontinalis antipyretica* Linn., *Hypnum elodes* Schp., *H. exannulatum* Guenbel, and other species, feeding on these mosses and probably on other plants. These moss fragments give a green tinge to young larvae when seen thru the nearly transparent body wall. Older larvae are more opaque and are brownish green in color, indistinctly striped with pale and darker. The larva is extremely sluggish, remaining almost motionless for hours. It clings to moss stems by its large anal hooks, and, thus secured, it often sways its body from side to side as if to accelerate respiration. The larvae can go for long periods of time without fresh air. Miall and Shelford kept specimens alive for two weeks in bottles completely filled with water, and for a long time in water that had been boiled. The larvae can live for a long time out of water. Progression thru the mats of submerged vegetation is accomplished by grasping with the mandibles and the anal hooks, alternately. When alarmed the larvae curl into a rounded ball, after the manner of many caterpillars. The skin, and more especially the long body processes, are often covered with ectoparasitic organisms, such as algae and infusoria, on which small fresh-water mollusks, Planorbis, have been observed feeding and creeping about over the body of the larva. This coating of organisms, the body outgrowths, and the general coloration of the larva, give it a striking resemblance to the mosses among which it lives. De Geer (1776:355) shows that the larva can endure excessive cold. He placed four larvae in a vessel at the beginning of winter, and examined them in the following May. During the winter

the water in which the larvae lived had frozen into a solid mass, yet, on investigating the jar in the spring, De Geer found two of the larvae still alive and able to feed, and within a month both had pupated.

The larval habitat is in ponds in which a moss vegetation flourishes and in which currents keep the water in constant motion. A female fly was observed by Miall and Shelford (1897:360) depositing her eggs in the leaf axils of a submerged moss. The eggs, about sixty in number, are laid singly and adhere slightly to the moss; they are opaque, dark in color, and spindle-shaped, with the surface of the chorion irregularly pitted, and with a rosette-like micropyle at one end. Bengtsson, Müggenberg, and others believe that Phalacrocera has but a single brood in a year, the larval existence occupying about eleven months; Miall and Shelford, however, admit the possibility of a second brood. The egg stage requires from eight to twelve days and the pupal duration is seven or eight days, according to Bengtsson. According to Miall and Shelford, the pupal period is considerably longer.

During the larval development there are numerous moltings, at least eight and possibly ten; the old larval skin is cast by a simple dorsal split extending from the first to the fourth segment. Just after emerging from the egg the larva is from 2 to 2.25 millimeters in length and about 0.5 millimeter in diameter, excluding the body projections. The first larval stage (Bengtsson, 1897) lasts until the second molting. The body is provided with ten pairs of long, delicate, threadlike, lateral projections, which are located on the second to the eleventh body segments and are half as long as the body. The other projections of the older larvae are merely indicated. The attachment apparatus is placed immediately before the anus, and consists of from eight to twelve chitinized hooks, directed forward and arranged in an arcuated crossrow. The color of the body is white, almost transparent. The mouth parts show the mandibles without a prostheca and moving horizontally. The second larval stage lasts from the second until the fourth molting. The body appendages have appeared and are clearly developed, resembling in appearance and relative length those of the definitive stage. The attachment apparatus is post-anal. The body takes on a distinctly striped appearance. The mouth parts have the prostheca well developed on the mandibles, which are vertically placed and therefore have an up-and-down movement. The third larval stage represents the fully grown larva from the fourth

molt up to the time of pupation. Here the dorsum of the body is a dirty brownish green with more or less distinct brighter spots, and the venter is bright green in color. The mouth parts and the attachment apparatus are as in the second stage.

The pupa is comparatively active, moving about by flexion of the abdomen. Its usual position is vertical, with the tips of the breathing horns just reaching the surface of the water. This vertical position the pupa maintains by grasping the vegetation with its caudal abdominal hooks. At times the pupa descends beneath the water by clinging to the vegetation, but a submergence of six hours causes asphyxiation. The pupal existence was determined by Miall and Shelford as eleven days. When the adult emerges, the cast pupal skin is left attached to a moss leaf by the dorsal abdominal projections at the posterior end of the body.

Larva.— Length, about 25 mm.

Young larvae distinctly greenish, especially on ventral side, this coloration caused, at least in part, by contents of alimentary canal showing thru body wall; older larvae more opaque, brownish green in color; dorsum with an indistinct striping of brown and whitish; ventral surface whitish.

Head entirely retractile within prothorax and usually so retracted except when larva is feeding; opening transverse. Prothorax, viewed from above, roughly rounded, anterior margin convex; on ventral surface traversed by a weak suture. Meso- and metathorax narrow. Abdominal segment 1 indistinctly divided into two annuli, the more basal one very narrow; abdominal segments 2 to 7 divided into a narrow basal ring and a much broader posterior ring, each of these annuli still further subdivided into two annulets. Body provided with numerous elongate trachea-bearing filaments, both simple and branched, giving larva a very bristly appearance (Plate LXXXIII, 448), these spines arranged as follows: *tergites* with both simple and bifurcated filaments; on posterior part of pronotum two short, simple filaments; on meso- and metanotum, two pairs of simple filaments; on abdominal segment 1, an anterior pair of simple, and a posterior pair of deeply branched, filaments; segments 2 to 7 with basal ring unarmed, posterior ring with an anterior pair of simple, and a caudal pair of deeply branched, filaments; segment 8 with only a branched pair, anterior branch long, slender, posterior branch very small, its outer face heavily chitinized and forming dorsal lobes of spiracular disk; *pleurites* with all the filaments simple; one on posterior part of prothorax, and on anterior part of each of the other two thoracic segments; posterior filament on these latter nearly vestigial; two unequal filaments on first abdominal segment; segments 2 to 7 with one filament on basal ring and two on posterior ring, the anterior one the longest; segment 8 with a single rudimentary filament; *sternites* with all the filaments simple; prosternum without filaments; meso- and metasternum with a strong filament near lateral margins; abdominal segment 1 with two pairs of filaments, posterior pair the longer and more widely separated; segment 2 with three pairs of filaments, anterior pair very short; segments 3 to 7 with four pairs of filaments and an additional median one, arranged as follows:

two pairs of small filaments on basal ring, the anterior pair more widely separated, two pairs of much longer filaments on posterior ring, the last pair more widely separated, longer, and tipped with blackish, between them a tiny median filament. Chaetotaxy as follows: tergites with four solitary setae along anterior margin of prothorax, and two setae just laterad of each dorsal filament of prothorax and posterior filaments of meso- and metathorax; abdominal segments with a seta laterad of each simple and branched filament; pleurites with a stiff seta at base, and out toward apices, of middle lateral filaments; sternites with a group of about four stiff setae on either side of posterior ring of prosternum, and a single stiff seta on either side of median line; meso- and metasternum with a lateral group of setae; a seta laterad, and another at about midlength, of each of the posterior pair of ventral filaments.

Spiracular disk with ventral lobes elongate, slightly recurved, the posterior face intensely blackened, chitinized, each lobe with two acute spines at tip, with two setae near them; a stiff seta on side of base of each ventral lobe; dorsal lobes as already described, the rudimentary posterior branch of last furcate dorsal filament much smaller than in ventral lobes, the posterior face heavily blackened; spiracular disk rhombic in form, white, and having almost the appearance of porcelain. Spiracles situated between bases of dorsal lobes. Skin about spiracles capable of retraction so as to form a deep recess.

Head capsule rather short, almost conical, formed of two large lateral plates and a somewhat smaller and shorter prefrontal plate. Mentum with an outer (ectolabial) part and an inner (endolabial) part; mentum a triangular or somewhat pentagonal plate, strongly chitinized, fore margin with about fifteen teeth; mandibles working against teeth of both endo- and ectolabia. Antenna of a single segment, bearing on its truncated apical end a few sensory papillae. Mandibles small but strong, curved inward at tip and furnished with a fringe of setae, which assist in closing the mouth opening. Maxilla expanded into flattened, shovel-like structures, inserted high on side of head; palpus with a number of sensory papillae at apex, and with a porous plate on outer side which seems to be an organ of hearing.

Pupa.— Length, 16–18 mm. (Miall gives length up to 20 mm.)
Width, d.-s., 2.9–3.3 mm.
Depth, d.-v., 2.7–2.9 mm.

Coloration greenish brown, in alcohol a paler yellowish brown; a very broad dorso-median dark brown stripe which is narrowly margined laterally with yellowish; dorsum of abdomen suffused sublaterally with dusky, extreme lateral margins of body yellowish; ventral surface with two broader sublateral stripes and a very narrow ventro-median stripe.

Anterior end of body very deep and thick, as is usual in this group of crane-flies. Abdomen greatly depressed, with lateral margins very thin and flattened. Cephalic crest low, non-setiferous, located between antennal bases. Labrum broad basally, narrowed toward apex, which is broadly rounded; two setae at base of labrum. Labial lobes subcircular in outline. Maxillary palpi elongate, bent strongly backward so as to lie along flattened cheek. Antenna rather elongated, extending far beyond origin of wing pad (Plate LXXXIII, 449). Thorax very deep, flattened above. Pronotal breathing horns, which are broken in the writer's specimens, seen from other descriptions to be rather elongate, almost straight, and slightly divergent; two small setae between bases of breathing horns; two groups of setae on anterior part of pronotum before breathing horns. Mesonotum (Plate LXXXIII, 449) with six

small, setiferous tubercles, one above each wing axil, the other four arranged in a trapezoid on dorsum with the anterior pair closer together; metanotum with six setiferous tubercles, four of which are median in position, the other pair at antero-lateral margin, near base of halteres. Wing sheaths ending about opposite apex of second abdominal segment. Leg sheaths ending before apex of third abdominal segment.

First abdominal segment similar to metanotum; segments 2 to 7 indistinctly subdivided into a narrow basal ring and a much broader posterior ring; basal ring unarmed except for a seta on pleural margin and a trapezoid of tubercles on sternum; posterior annulus armed as follows: tergites with four tubercles arranged in a quadrangle and located in the dark median stripe, posterior tubercles with a stiff seta just laterad of each; a lateral seta on a line with anterior tubercles; two lateral setae on a level with posterior tubercles, the proximal one considerably the larger; these setae located in the yellow sublateral stripe; pleural margin with two setiferous tubercles with an acute subappressed spine between them; a seta immediately ventrad of anterior tubercle; on segments 6 and 7, spine closer to caudal margin of segment, and tubercle beyond it lacking; sternites with a trapezoid of naked tubercles on basal ring, posterior pair the closer together; a trapezoid of larger setiferous tubercles on posterior ring, anterior pair the closer together; posterior punctures each having two setae with an additional slender seta laterad of these in the lateral dark stripe; dorsum of segment 6 (Plate LXXXIII, 450) with posterior pair of tubercles replaced by two powerful lobes directed caudad and laterad; segment 7 unarmed on dorsum, sternum with two acute spines near caudal margin; segment 8 with lateral angles produced dorsad into slender lobes which are spinous on all the faces; caudal angles directed caudad into slender lobes, acute at tips and with anterior inner face spinous and bearing a few setae. Male cauda with sternal valves very blunt and rounded, on either side of ventro-median line produced caudad into an acute spine. Female cauda with dorsal acidothecae a little longer than the more slender sternal valves, both pairs much exceeded by caudal angles of eighth segment.

Nepionotype.— Larva, Denmark.
Neanotype.— Pupa, Denmark.
Paratypes.— One larva and one pupa.

(The writer is indebted to Dr. C. Wesenberg-Lund for this material as well as for several other interesting European crane-fly life histories.)

Genus **Cylindrotoma** Macquart (Gr. *cylinder* + *I cut*)

1834 *Cylindrotoma* Macq. Suit. à Buff., vol. 1, Hist. Nat. Ins., Dipt., p. 107.

Larva.— Body covered with simple tubercles, a median dorsal row and a double ventral row. Spiracular disk large, surrounded by small lobes. Head capsule compact. Mentum with about fifteen teeth.

Pupa.— Pronotal breathing horns short, cylindrical, directed strongly ventrad. Mesonotum with two flattened lobes directed cephalad. Abdomen unarmed with spines or lobes.

Cylindrotoma is a small genus including six species distributed thruout the North Temperate Zone, three of these species occurring in North America.

The adult flies of *Cylindrotoma tarsalis* Johns., the only species that the writer has ever found in nature, are common on rank vegetation in cool, boggy, and swampy woods. The immature stages of the genotype, *C. distinctissima* (Meig.), have long been known, having been discussed by Schellenberg (1803), Boie (1838), Zeller (1842), Kaltenbach (1874), and others. The larva shows some resemblance to that of Phalacrocera, but is almost entirely terrestrial in its habits, feeding on the leaves of various spermatophytic plants such as *Caltha palustris, Anemone nemorosa, Ranunculus repens,* Chrysosplenium, *Stellaria nemorum, Sanicula europaea, Viola biflora, Valeriana officinalis,* Allium, and others. It attains a length of nearly 25 millimeters, and is narrow, depressed, tapering to either end, and of a grass-green color. There is a slight dorsal ridge from which a row of short, fleshy spines projects, these spines being directed backward and one spine on each segment being longer than the others. There is a broad lateral margin bearing very short processes, and there are also eight pairs of ventral ridges without hooks and a pair of longer backward-directed processes near the anus. The pupa affixes itself to stalks or leaves by the caudal end, to which the remains of the last larval skin adhere. The larvae generally remain on the lower surface of the leaves, on which they feed, gnawing holes in them. When about to pupate they generally leave their food plants and fasten themselves on grass blades and leaves near by, usually pupating the following day. From the foregoing observations it would seem that there are in the various localities two generations a year, one in the spring and the other in the autumn.

The life history of *C. splendens* has recently been worked out in considerable detail by Dr. A. E. Cameron, thru whose kindness the writer has received specimens for study.

Cylindrotoma splendens Doane

1900 *Cylindrotoma splendens* Doane. Journ. N. Y. Ent. Soc., vol. 8, p. 197.
1900 *Cylindrotoma juncta* Coq. Proc. Wash. Acad. Sci., vol. 2, p. 401.
1918 *Cylindrotoma splendens* Cameron. Ann. Ent. Soc. Amer., vol. 11, p. 67–89.

Cylindrotoma splendens is an interesting crane-fly occurring from British Columbia northward to Alaska. Dr. Cameron's excellent notes on the life history of this species are abstracted in detail on pages 708 to 710 of this paper. The following descriptions were made from material sent

to the writer by Dr. Cameron, a few details being added from Dr. Cameron' published notes.

Larva.— Length, 15–17 mm.
Width, d.-s., 2.4–2.5 mm.
Depth, d.-v., 1.5 mm.

Coloration light chlorophyll green, with two narrow, pale brown lines on dorsum, extendin from posterior end, above spiracles, anteriorly, becoming more expanded and diffused o fore part of body.

Body very depressed, both dorsal and ventral surfaces being flattened, lateral margi sharp (Plate LXXXIV, 453). Head completely retractile within prothorax. Skin delicatel reticulated and roughened. Thorax, viewed from above, semicircular in outline, margin with about four tubercles on either side, anterior pair the largest, separated by a V-shap notch. Pronotum with an anterior pair of small tubercles and a larger median tuberc behind, directed backward; segments 2 and 3 each with lateral margins two-toothed, t anterior tooth the larger and more pointed; a blunt dorsal tubercle on anterior margin a a larger one behind. Abdominal segments indistinctly divided into four annuli which a poorly delimited; the two basal annuli narrow and corresponding to basal annulus of mo crane-fly larvae, the third annulus the largest and bearing a slender lateral tooth; oth segments less distinctly divided serrately on lateral margin; dorsum of abdominal segmen with a row of blunt median tubercles, there being four on each segment, the first very sm to vestigial, the third slender, the last the stoutest; on venter of abdominal segments 1 7, near posterior margin, a fleshy conical lobe (pseudopodium) on either side of median li these being smaller on anterior segments (1 to 4), and much larger and paler on posteri segments (5 to 7). Spiracular disk very large and flattened, obliquely truncated, surround by six small lobes, the dorso-lateral pair small, widely separated, the ventro-lateral p much larger, the ventral pair very small, slender. Spiracles very small, circular, wide separated, the distance between them about equal to six times diameter of one.

Mouth parts with labrum linguliform, terminating in four teeth, external pair small than internal pair. Mentum with seven teeth on either side of small median one, the fi and the third on either side being the largest. Hypopharynx with two rows of small teet Antenna two-segmented; basal segment elongate, pyriform; apical segment thimble-shap Mandible (Plate LXXXIV, 454) powerful; cutting edge with about five marginal teeth a two dorsal teeth; a large basal prostheca. Maxilla large; outer lobe fringed with stiff hai a few acute sensory bristles situated on elevated papillae, two on cardo, one on outer lo of maxilla; maxillary palpi short, cylindrical, apex obliquely truncated and provided wi numerous sensory knobs, on side near tip a circular porous plate (which as it appears Phalacrocera is suggested by Bengtsson as probably being an organ of hearing).

Pupa.— Length, 11.7–14 mm.
Width, d.-s., 2–2.8 mm.
Depth, d.-v., 1.4–2 mm.

Color of live pupa, leaf green; preserved specimens much paler, yellowish; prono breathing horns grayish white; margins of abdomen nearly translucent.

Labrum narrow, apex evenly rounded. Labial lobes stout, separated by labrum, at tip arrowed and somewhat pointed. Maxillary palpi long and stout, just beyond base bent trongly backward. Antennae rather short, bases not widely separated (Plate LXXXIV, 56). Thorax very deep, much flattened anteriorly (Plate LXXXIV, 455). Pronotal reathing horns short, cylindrical, slightly divergent, apex of each a little expanded. Meso-otum at declivity with two flattened plates, which are blunt and directed cephalad and lightly laterad; above wing axil a smaller tubercle. Wing sheaths ending just before apex f second abdominal segment. Leg sheaths ending just before apex of third abdominal egment; tarsi ending about on a level.

Abdomen strongly depressed, lateral margins carinate; segments distinct, unarmed, sub-ivided into a narrow basal ring and a much broader posterior ring; segments 2 to 5 a little onger than segments 6 and 7. Male cauda with valves divided into two rounded lobes y a small median notch. Female cauda with dorsal valves straight, a little longer and uch stouter than the slender sternal valves.

Nepionotype.— Westholme, Vancouver Island, B. C., May 15, 1917.
Neanotype.— Female pupa with type larva.

Genus **Liogma** Osten Sacken (Gr. *smooth* + *furrow*)

1869 *Liogma* O. S. Mon. Dipt. N. Amer., part 4, p. 298.

Larva.— Body covered with elongate, leaflike projections, dorsal ones with one or two eeth on anterior convex face. Spiracular disk surrounded by four lobes. Head capsule ompact. Mentum with about fourteen teeth.

Pupa.— Metanotum and abdominal tergites with elongate spines, branched in *L. glabrata*, imple in *L. nodicornis*.

The genus Liogma includes three known species, of which the genotype, *Liogma nodicornis* (O. S.), is American. The adult flies of this species re sluggish, and are found resting on vegetation growing in and about haded ponds and similar situations.

In Europe the life history of *L. glabrata* (Meig.) has been worked out y De Rossi (1876), by Wesenberg-Lund (1915:347–348), and in con-iderable detail by Müggenberg (1901). The larvae were found in the voods near Berlin, in wet, grassy spots where the moss *Hypnum squarrosum* Brch. & Schp. occurs. The complete metamorphosis of the insect takes ne year, the larval life requiring the greater part of this period. The gg stage lasts from eight to ten days and the pupal stage from eleven to welve days. The duration of adult life is not known, but it is certainly hort, occupying but a few weeks at the most.

Near Berlin the flies emerge during the first half of July. The males ppear first, the females later, and the latter are always seized in copulation

by the males just after they have forsaken the pupal skin and while still teneral and undeveloped. Each female lays about sixty eggs, and these are deposited singly on the leaves or branches, or attached lightly to the axils of the leaves, of *Hypnum squarrosum*. Egg deposition begins from one-half to one day after copulation, and may be extended, with many interruptions of greater or less extent, thru a whole day. The eggs are from 1 to 1.2 millimeters long, spindle-shaped, yellowish green in color, the chorion with a reticulate sculpturing. After the accomplishment of oviposition the exhausted female soon dies. The larvae when first hatched are 2 millimeters in length and do not yet possess the beautiful moss-green color of the later stage. With the exception of the chitinized head capsule, they appear ashy gray. The numerous thornlike projections are to be noted already in the same positions as those of the developed larva, but do not show the branching of the later stages. In the autumn the young larva grows very slowly, and during the winter it is still very small and difficult to detect. In the spring the growth is greatly accelerated, and the larva becomes fully grown during the latter half of June. While attaining its growth the larva molts several times, probably at least eight — the number determined for Phalacrocera by Bengtsson. Pupation occurs in the moss where the larva happens to be. In its green color, with brown blotches, the larva remarkably simulates its host plant and the effect of the shadows cast by the plant stems and leaves. The larvae are extremely sluggish in their habits.

The American species *Liogma nodicornis* has been found in various mosses of the genus Hypnum (Alexander, 1914). The immature stages of this species are discussed below.

The following keys separate the species of Liogma:

Larvae

Prothoracic segment bearing four conspicuous dorsal projections about on a line; meso- and metathorax with two pairs of dorsal appendages, each bearing two lateral teeth in front; second abdominal segment with four dorsal appendages, the last two bearing two teeth in front (Palaearctic) . . . . *glabrata* (Meig.) (p. 969)

Prothoracic segment bearing four inconspicuous dorsal tubercles; meso- and metathorax with two pairs of dorsal appendages, the anterior pair small, both pairs simple; second abdominal segment with four dorsal appendages, the last two bearing a single small tooth in front (Nearctic) . . . . *nodicornis* (O. S.) (p. 971)

Pupae

Pronotal breathing horns directed cephalad and dorsad; mesonotum bearing two pairs of spines, the more anterior being the smaller, situated just behind breathing horns, posterior pair the larger; metanotum with two pairs of spines; abdomen with first tergite bearing two pairs of spines, the first having two lateral branches, the second simple; second tergite bearing two pairs of spines, the first with two lateral branches, the second with one branch; third tergite bearing three pairs of spines, the first very short and simple, the second with two lateral branches, the third with one branch; tergites 4 and 5 with three pairs of branches, the first two similar to those of third segment, the last possessing two lateral branches.. *glabrata* (Meig) (p. 969)

Pronotal breathing horns directed cephalad and ventrad; mesonotum spineless; metanotum with one pair of spines; abdominal tergites bearing but a single pair of appendages, which are unbranched and correspond in position to the last or more posterior of those of the European species... *nodicornis* (O. S.) (p. **971**)

Liogma nodicornis (O. S.)

1865 *Triogma nodicornis* O. S. Proc. Ent. Soc. Phila., vol. 4, p. 239.
1869 *Cylindrotoma nodicornis* O. S. Mon. Dipt. N. Amer., part 4, p. 301.
1887 *Liogma nodicornis* O. S. Berl. Ent. Ztschr., vol. 31, p. 226.

Liogma nodicornis, the only American species of the genus, is widely listributed thruout the Northeastern States. The larvae are found in moss — *Hypnum cupressiforme* Linn. and related species. They are the most sluggish of any crane-flies known to the writer, moving only with great slowness and much of the time appearing to be quite dead. They crawl about among the stems of their host plant and probably never leave it, even to pupate. The pupal duration indoors is not more than six days. Further details of the life history are given by the writer in an earlier paper (Alexander, 1914).

Larva.— Length, 14.5–15 mm.
Width, 3 mm.
Depth, 2.5 mm.

Color of live larva light green, the numerous spines covering the body darker; sides with seven black marks, the first on first abdominal segment, the last on seventh abdominal segment; the marks on ends the smallest and least distinct, the five intermediate marks large and conspicuous; these marks all lying parallel to one another; posterior face of ventral lobes surrounding stigmal field intensely black.

Prothorax in front (Plate LXXXV, 462) sloping from anterior end, on ventral slope provided with liplike lobes, with a transverse slit from which head capsule is exserted; upper lip the higher, not strongly chitinized, provided with a few small, scattered bristles, these more numerous on sides of lobe; lower lip not so high, with small, scattered bristles not arranged in a row as in *L. glabrata*; at angle of slit a small rounded lobe bearing a small bristle. Dorsal body appendages reduced to a pair of lobes in front, separated by a space a little greater than diameter of one, and a pair of smaller lobes behind, very widely separated; lateral body appendages long, conspicuous; ventral body appendages not apparent. Meso- and metathorax swollen and arched ventrally like prothorax; dorsal appendages two, a small conical

one in front and a much larger one behind bearing a small tooth in front and with its tip directed backward; lateral appendages, viewed from above, two in number, anterior one the larger, directed sharply backward, the second smaller, conical; ventral appendages, viewed from side, four, anterior pair the larger, posterior pair small, slightly behind the others.

Dorsal appendages of abdominal segments (Plate LXXXV, 457) as follows: first segment with two pairs of appendages; anterior pair the shorter, conical, tips strongly recurved and bearing a tiny tooth on anterior face at about midlength; posterior pair much longer, with tips bent strongly backward, a small tooth on anterior face at about one-third length from base; segments 2 to 7 with four pairs of appendages, the first pair very small, conical, the second exactly similar but larger, the third and fourth pairs similar to appendages of first abdominal segment; the tiny anterior appendage largest on second segment, gradually becoming smaller toward end of body. Lateral abdominal appendages as follows: first segment with three pairs of appendages, the first directed laterad, the posterior two more recurved and directed caudad; segments 2 to 7 with four pairs of appendages, the first very small, situated at antero-lateral angle of segment, the other three subequal and directed caudad. Ventral abdominal appendages as follows: first segment with three pairs of appendages, which are successively larger from the short anterior one to the large posterior one; segments 2 to 7 with five pairs of appendages, the first three small, the fourth intermediate in size between them and the enlarged fifth pair. Eighth segment bearing spiracular disk and its lobes; dorsal side of field with a pair of long, slender lobes bent conspicuously cephalad. Spiracular disk (Plate LXXXV, 461) small, oval, the two rounded-oval spiracles situated side by side and close to each other, inclined toward each other and capable of being closely appressed; ventral lobes of disk directed ventrad, inner faces of lobes with a conspicuous jet-black line, tip of each lobe ending in a sharp recurved hook. (Müggenberg regards these lobes as representing the ninth abdominal segment.) Ventral surface of terminal segments with small protuberances.

Head completely retractile into first thoracic segment. Mentum (Plate LXXXV, 458) with about seven teeth on either side, terminal pair the larger, separated by a V-shaped notch. Antenna (Plate LXXXV, 460) two-segmented, basal segment elongate-cylindrical, tip very short, thimble-shaped, with a diameter less than that of elongate basal segment. Mandible (Plate LXXXV, 459 and 460) many-toothed on inner face, with a prominent basal prostheca; mandibles working vertically against teeth of mentum. Maxilla (Plate LXXXV, 458) with palpi very short, broad, basal segment chitinized, tip narrow, pale.

Pupa.— Length: male, 10.4–11.4 mm.; female, 10–13 mm.
Width, d.-s.; male, 2–2.2 mm.; female, 2.2–2.6 mm.
Depth, d.-v ; male, 1.9–2.2 mm.; female, 2.1–2.5 mm.

Living pupae with pronotal breathing horns light yellow, the terminal half a little more brownish; a brownish black mark on prescutum; abdomen greenish, more yellow behind; dorsal spines clear light green thruout or with tips in some specimens a little infuscated. (In pupae preserved in alcohol, the greenish colors are lost, the dark brownish black mark of the mesonotal prescutum is irregularly U-shaped, with the arms of the U directed backward, and the dark color is produced caudad and cephalad along the dorso-median line; there is a triangular or rounded black spot on either side of the scutellar lobe; on the metanotum is a large blackish median blotch, which is continued cephalad onto the mesonotal postnotum; the abdomen has an interrupted brownish black longitudinal line along either side of the midline of the dorsum; the posterior margin of each tergite is suffused with

brown.) In old and fully colored pupae, bases of dorsal spines brown, with the tips paler; head and thorax with appendages brown, in some specimens very dark; abdomen yellowish.

Cephalic part of head very flat and broad, without spines but with a small, blunt tubercle between antennal bases. Labrum transversely wrinkled, narrowed to the bluntly rounded apex. Labial lobes large, divergent, each lobe rectangular with angles rounded. Sheaths of maxillary palpi rather long, curved strongly backward. Antennal sheaths rather enlarged, directed cephalad, bending around anterior margin of eye and thence directed caudad, ending just beyond knee joint of fore legs. (In older pupae, the peculiar nodose antennal segments of the adult show thru the sheath.) Pronotal breathing horns (Plate LXXXV, 464) large, conspicuous, directed dorsad and laterad, the terminal half bent rather suddenly cephalad. Mesonotum transversely wrinkled. Metanotum (Plate LXXXV, 463) with two long, slender spines, arising beyond midlength of segment, directed caudad and slightly dorsad. Wing sheaths broad, reaching posterior margin of second abdominal segment. Leg sheath ending just before posterior margin of third abdominal segment; fore legs the shortest, hind legs the longest.

Abdominal segments with a narrow basal ring and a broader posterior ring; segment 1 about half as long as segment 2; tergites 1 to 7 with a pair of long, slender, spinous projections, shortest on anterior segment, longest on seventh segment, these projections arising from near caudal margin of segment, directed dorsad and caudad, those of anterior segment almost parallel, those of posterior segments more divergent; segments 2 to 7 having lateral margins produced into three sharp spines, one on basal ring and two on posterior ring of each segment, these spines directed laterad and caudad, the terminal spines more sharply caudad than the other two; abdominal sternites armed as follows: segment 3 with a small, subapical spine on either side, these spines very widely separated, segment 4 with similar spines but larger and more prominent, segments 5 to 7 similarly armed but with another pair of small spines about midlength of segment and much nearer midline of body, segments 2 to 7 with a subbasal triangular pit on either side, these pits widely separated; eighth tergite with caudal margin rounded, concave, the lateral angles produced backward, upward, and slightly outward as strong spines; suture on ventral surface incomplete; two small spines on either side of middle line of body; posterior margin of segment produced caudad as two strong spinous projections. Male cauda with sternal valves rather long, tipped with two to four acute spines, in some specimens with two spines on one of the lobes and only one on the other; tergal valves a little rounded at tips, slightly longer than sternal valves. Female cauda (Plate LXXXV, 465 and 466) with sternal valves slender, feebly notched at tips; tergal valves broader, rounded at tips, and with a deep median split.

Nepionotype.— Coy Glen, Ithaca, New York, May 8, 1913.
Neanotype.— Ithaca, May 30, 1913.
Paratypes.— Larvae and pupae with types; others from Orono, Maine, June 17 and 19, 1913.

Genus **Triogma** Schiner (Gr. *three + furrow*)

1863 *Triogma* Schin. Wien. Ent. Monatschr., vol. 7, p. 223.

Larva.— Body covered with elongate leaflike projections, some of the dorsal ones with as many as four teeth on anterior convex face. Spiracular disk surrounded by four lobes.
Pupa.— Dorsum of abdomen with elongate branched spines.

The genus Triogma includes but three known species, the genotype *Triogma trisulcata* (Schum.) of Europe, *T. kuwanai* (Alex.) of Japan, and *T. exculpta* O. S. of the eastern United States. The last-named species is very rare and its habits are entirely unknown.

The first reference to the immature stages of *T. trisulcata* is by Steinmann (1907–08), who discusses the larva as that of an unknown species of Phalacrocera. The true identity of this insect was made known by Müller (1908–09). Steinmann found the larvae at Säckingen at the end of April, fourteen days after the melting of the snow. They were found in mountain streams, attached to and living among the stems of the aquatic moss *Fontinalis antipyretica* Linn., to which they clung firmly by means of two strong chitinized hooks at the caudal end of the body. The larva resembles to a startling degree the moss on which it lives. Along the dorsal surface are two rows of leaflike appendages, each of the abdominal segments having three such appendages, of which the most anterior one is the shortest and the posterior one is the longest. The anterior appendage is untoothed, the others have as many as four teeth on the anterior face. The pleural region likewise bears a row of leaflike structures, while the ventral surface shows a double row of small, knoblike leaflets. Thru the strong accentuation of the dorsal and the two lateral rows, there is produced a copy of the ternate condition of the leaf arrangement in Fontinalis.

The larva of *T. trisulcata* (Plate LXXXIII, 452) is of a light green color marked with darker blotches, and measures 19 millimeters in length. The longest body appendage is 1.5 millimeters in length. Müller found larvae and also pupae. The pupa is characterized by the possession of somewhat similar appendages to those of the larva, the dorsal row showing the peculiar branched condition found in the larva.

SUBFAMILY **Tipulinae**

The subfamily Tipulinae comprises a remarkably homogeneous assemblage of usually large species. It is made up of a relatively few but in some cases very extensive genera, which are found thruout the world. Efforts have been made in the past to maintain three tribes — the Dolichopezini, the Ctenophorini, and the Tipulini. It has become increasingly difficult, however, to define these groups on the constant accession of exotic genera and species. A study of the immature stages likewise

ails to substantiate the validity of these groups, and, for the present t least, or until other and better characters may be found, it is better o eliminate the Dolichopezini and the Ctenophorini, founded, as they re, on insufficient or sexual characters.

The species of the Tipulinae include the largest crane-flies known, some xotic species of Ctenacroscelis attaining a wing expanse of nearly 10 entimeters. In North America the largest species are representatives f the genera Longurio and Holorusia. The great majority of the species n this subfamily are well above the average in size, this feature alone eing sufficient to eliminate all but a very few of the other groups of 'ipulidae. The smallest member of the subfamily Tipulinae known to he writer is *Microtipula amazonica* Alex., of Brazil, in which the wing of he male measures but 7.2 millimeters in length and is very long and arrow. Practically all of the common local species of this group belong o the two genera Tipula and Nephrotoma.

The immature stages of members of the subfamily Tipulidae are found n a wide range of habitats. Some species of Tipula are almost entirely quatic in the larval state. The majority of the known species live in noist earth near water, or beneath damp cushions of moss. Some, such s Oropeza, live in much drier mosses on exposed rocks. A rather con-iderable number of species (Brachypremna, Ctenophora, Dictenidia, and everal species of Tipula) live in decaying wood or beneath the bark of rostrate trunks. Tanyptera lives in wood which is relatively sound, nd this represents the extreme development of this tendency in the amily.

The larvae are never very slender, and are usually very plump and erete. In a few cases only is the body decidedly depressed. There is definite arrangement of setae on the body, there being none on the nterior annulus of the abdominal segments except a single seta on the leura of either side. The spiracular disk is surrounded by six lobes, number not found in the Limnobiinae. In Dolichopeza the number s described as being five, the normal number in the Eriopterini, but ll other features of the genus are essentially tipuline. In a few species he number of lobes is increased to eight. In the genus Tanyptera the obes are exceedingly reduced in size so that the caudal end appears almost aked and exposed. The spiracles are always present and in some cases re very large. The anal gills are almost always present and are variously

developed according to the habitat. The head capsule is remarkabl uniform thruout the group, being broad, compact, and massive, with th posterior incisions shallow and the prefrontal sclerite very large an usually distinct. The labrum is usually conspicuous, transverse, wit fringes of hairs. The mentum has from seven to nine teeth along th anterior margin, and is deeply split behind but not completely divide The hypopharynx consists of a narrow, flattened plate, with the basa lateral angles produced into strong arms and the anterior margin havin usually five teeth, the teeth being rarely more numerous and in som cases obsolete. The antennae are cylindrical, and are stoutest in th wood-inhabiting species; in many species of Tipula and Prionocera the are long and slender, the length being about four times the diamete the apical papilla, in some cases obsolete, is usually very small and i flattened. The mandibles are not large in proportion to the size o the capsule; they have few teeth, in some species only a dorsal and ventral tooth in addition to the apical point; the prosthecal appenda is variously developed. The maxillae are simple and generalized i structure.

The pupae are fairly uniform in structure thruout the subfamily. Th tips of the sheaths of the maxillary palpi are strongly curved, or, in th majority of species, actually recurved. The pronotal breathing horns a variously formed, but in practically all species they are short, cylindrica and with the tips but little expanded. In some genera (Longuri Prionocera, and Tipulodina) the breathing horns are greatly elongate and, in some cases at least, are slightly unequal in length, the long measuring nearly half the length of the body. In some genera, suc as Prionocera and Holorusia, the horns are split at their tips into tw divergent flaps. The only short, clavate horns in the subfamily a those of the genus Tanyptera. The mesonotum is often provided wit four or six variously developed tubercles. The abdominal segments a almost always armed with transverse posterior rows of spines, the ranging in number from about four to twenty.

The large size of the larvae and the pupae will, as a rule, easily separa this subfamily from almost all members of the Limnobiinae. The fe large members of the latter group are readily separated by the characte outlined above.

The following keys separate the genera of the subfamily Tipulinae:

Larvae

1. Spiracular disk surrounded by five lobes; living in moss....... *Dolichopeza* Curt. (p. 981)
Spiracular disk surrounded by four or six lobes, or with lobes indistinct...............2
2. Spiracular disk with lobes indistinct; living in nearly solid or semi-decayed wood. *Tanyptera* Latr. (p. 988)
Spiracular disk with lobes distinct...3
3. Spiracular disk with four slender, hornlike lobes.......... *Tipula* (*selene* Meig.) (p. 1016)
Spiracular disk with six lobes...4
4. Anal gills pinnately branched............................*Longurio* Loew (p. 990)
Aeshnasoma Johns. (p. 993)
Anal gills not pinnately branched..5
5. Antepenultimate segment of abdomen with a strong lateral tubercle. *Oropeza* Needm. (p. 982)
Antepenultimate segment of abdomen without such a tubercle......................6
6. Dorsum of head behind antenna with a slender, flexible spine; living in wood. *Ctenophora* (*apicata* O. S.) (p. 986)
Dorsum of head without such a spine...7
7. Lobes surrounding spiracular disk elongate, digitiform, fringed with long hairs. *Prionocera* Loew (p. 995)
Lobes surrounding spiracular disk less elongate..................................8
8. Size large (over 50 mm.); spiracular disk with the six moderately long lobes fringed with long hairs; mandible small, with a dorsal and a ventral tooth; found in western North America...*Holorusia* Loew (p. 993)
Size smaller; if large (*T. abdominalis*), the lobes surrounding disk bifid; mandible with two or three ventral teeth...............................*Tipula* Linn. (p. 998)
Nephrotoma Meig. (p. 1016)

Pupae

1. Pronotal breathing horns very long, slender, the longest one nearly if not quite half length of body...2
Pronotal breathing horns short, cylindrical or flattened, subequal in size.............3
2. Length 40 mm.; longest breathing horn 18 mm.; maxillary palpi not recurved at tips; venation with petiole of cell M_1 very short...................*Longurio* Loew (p. 990)
Length 20 mm.; longest breathing horn 9 to 10 mm.; maxillary palpi recurved at tips; venation with petiole of cell M_1 longer...................*Prionocera* Loew (p. 995)
3. Pronotal breathing horns short, compressed, deeply bicrenulated; living in wood. *Tanyptera* Latr. (p. 998)
Pronotal breathing horns cylindrical..4
4. Maxillary palpi not recurved at tips..5
Maxillary palpi recurved at tips..6
5. Pronotal breathing horns with apices deeply split; mesonotum with two tubercles; abdominal segments with fourteen to thirty-four spines; found in Western States; living in mud...*Holorusia* Loew (p. 993)
Pronotal breathing horns short, slender, apices not split; mesonotum with eight tubercles; abdominal segments with four powerful spines near posterior margin; found in Southern States; living in wood.................................*Brachypremna* O. S. (p. 984)
6. Mesonotum with two spines; ventral abdominal spines six to eight; fore and middle tarsi subequal, shorter than hind tarsi; living in wood...........*Ctenophora* Meig. (p. 986)
Characters not as above...7
7. Mesonotum with a large, roughly triangular, reticulated area on either side of median line; dorsum of cauda with four lobes.....................*Oropeza* Needm. (p. 982)
Mesonotum unarmed or with four or six lobes; dorsum of cauda with six, or rarely four, lobes...*Tipula* Linn. (p. 998)
Nephrotoma Meig. (p. 1016)

The most important literature on the Tipulinae is as follows:

Dolichopeza albipes	Pupa	Beling, 1879:44–45 (as *sylvicola*).
Dolichopeza albipes	Larva, pupa, general	Beling, 1886:189–191 (as *sylvicola*).
Tanyptera atrata	General	Perris, 1840:92; 1849:333.
Tanyptera atrata	General	Nördlinger, 1848.
Tanyptera atrata	General	De Rossi, 1882.
Tanyptera atrata	Larva, pupa, general	Gercke, 1884, Pl. I, figs. 12–19.
Tanyptera atrata	General	Hermann, 1880.
Tanyptera atrata ruficornis	Larva	Gerbig, 1913:156–158 (as *Ctenophora flavicornis*).
Tanyptera fumipennis	Larva, pupa, general	Malloch, 1915–17 b:194–195; 1919.
Dictenidia bimaculata	Larva	Bouché, 1834:32.
Dictenidia bimaculata	General	Zetterstedt, 1851:4023.
Dictenidia bimaculata	Larva, pupa, general	Weyenbergh, 1872.
Dictenidia bimaculata	General	Beling, 1873 b:575.
Dictenidia bimaculata	General	Czizek, 1913:102.
Ctenophora flaveolata	Larva, pupa, general	Réaumur, 1740, Pl. I, fig. 9.
Ctenophora flaveolata	General	Zetterstedt, 1851:4016.
Ctenophora flaveolata	Larva, pupa, general	Weyenbergh, 1872.
Ctenophora pectinicornis	Larva, pupa	Bouché, 1834:29–31.
Ctenophora pectinicornis	General	Fischer von Waldheim, 1838.
Ctenophora pectinicornis	Larva, pupa	Weyenbergh, 1872.
Ctenophora pectinicornis	General	Zetterstedt, 1851:4014.
Ctenophora pectinicornis	General	Kaltenbach, 1874:202.
Ctenophora festiva	Larva	Kaltenbach, 1874:631.
Ctenophora festiva	Larva	Czizek, 1911:48.
Ctenophora nigricoxa	Pupa	Lundström, 1906:7.
Ctenophora apicata	Larva, pupa	Johannsen, 1910:32–33.
Ctenophora angustipennis	Larva, pupa, general	Anthon, 1908.
Ctenophora angustipennis	Egg, larva, pupa, injury.	Lovett, 1915.
Aeshnasoma rivertonensis	Larva	Johnson, 1906:1–2.
Aeshnasoma rivertonensis	General	Johnson, 1907–12 [1909]:115–116.
Tipulodina pedata	Pupa	De Meijere, 1911:64.
Holorusia rubiginosa	Larva, pupa, general	Kellogg, 1901, a and b.
Holorusia rubiginosa	Larva	Comstock and Kellogg, 1904: 54–62.
Prionocera fuscipennis	Larva, pupa, general	Malloch, 1915–17b:199–200.
Prionocera parri, supp (Palaearctic species)	Larva	Alexander, 1919 c.
Tipula caesia	General	Schiner, 1864:516.
Tipula dilatata	Larva, pupa	Beling, 1886:176.
Tipula dilatata	Larva, pupa	Czizek, 1913:169.
Tipula flavolineata	General	Staeger, 1840:23.
Tipula flavolineata	Larva, pupa	Beling, 1873 b:581–582.
Tipula flavolineata	Larva, pupa	Czizek, 1913:146.
Tipula fulvipennis	Larva, pupa	Beling, 1879:22–24 (as *lutescens*).
Tipula fulvipennis	Larva, pupa	Czizek, 1913:74.
Tipula hortensis	Larva, pupa	Beling, 1873 b:578–579.
Tipula hortensis	Larva	Gerbig, 1913:154–156.

Tipula hortulana	Larva, pupa, general	Beling, 1879:25; 1886:178–179.
Tipula hortulana	Larva, pupa, general	Czizek, 1913:96.
Tipula imbecilla	General	Loew, 1869:9.
Tipula irrorata[7]	Larva, pupa	Beling, 1873 b:586–587.
Tipula irrorata	Larva, pupa	Czizek, 1913:98–99.
Tipula lateralis	Larva, pupa	Beling, 1879:26–28.
Tipula lateralis	Larva	Gerbig, 1913:153–154.
Tipula lateralis	Larva, pupa	Czizek, 1913:128.
Tipula lateralis	General	Cameron, 1917:61.
Tipula lunata	Larva, pupa	Brocher, 1909.
Tipula luteipennis	Larva, pupa	Beling, 1886:181–182.
Tipula luteipennis	Larva, pupa	Czizek, 1913:143.
Tipula marmorata	Larva, pupa	Beling, 1886:182–183.
Tipula maxima	Larva, pupa	Beling, 1886:177–178 (as *gigantea*).
Tipula maxima	Larva	Gerbig, 1913:152–153 (as *gigantea*).
Tipula maxima	Larva, pupa	Czizek, 1913:70–71.
Tipula maxima	General	Wesenberg-Lund, 1915:335 (as *gigantea*).
Tipula micans[7]	Larva, pupa	Beling, 1886:183–184.
Tipula nigra	Larva, pupa	Beling, 1879:28–29.
Tipula nigra	Larva, pupa	Czizek, 1913:132.
Tipula nubeculosa	Larva, pupa	Beling, 1873 b:575–577.
Tipula nubeculosa	Larva, pupa	Czizek, 1913:113.
Tipula ochracea	Larva, pupa	Beling, 1873 b:582–583.
Tipula ochracea	Larva, pupa	Czizek, 1913:157.
Tipula oleracea	Larva, pupa	Del Guercio, 1914.
Tipula oleracea	General	Patterson, 1908.
Tipula pabulina	Larva, pupa	Beling, 1873 b:579–580.
Tipula pabulina	Larva, pupa	Czizek, 1913:86.
Tipula pagana	Larva, pupa	Beling, 1879:29–31.
Tipula paludosa	Larva, pupa	Beling, 1873 b:583–585.
Tipula paludosa	Larva	Gerbig, 1913:136–151.
Tipula paludosa	Larva, pupa	Czizek, 1913:136.
Tipula paludosa	Larva, pupa	Rennie, 1916; 1917.
Tipula parva, supp	General	Onuki, 1905.
Tipula peliostigma	Larva, pupa	Beling, 1879:33–34.
Tipula peliostigma	Larva, pupa	Czizek, 1913:159.
Tipula pruinosa	Larva, pupa	Beling, 1879:31–32; 1886:184.
Tipula pruinosa	Larva, pupa	Czizek, 1913:148.
Tipula rufina	Larva, pupa	Mik, 1882 a.
Tipula scripta	Larva, pupa	Beling, 1873 b:577–578.
Tipula scripta	Larva, pupa	Czizek, 1913:110.
Tipula selene	Larva, pupa	Beling, 1879:34–35.
Tipula selene	Larva, pupa	Czizek, 1913:160–161.
Tipula signata	Larva, pupa	Beling, 1879:32–33.
Tipula signata	Larva, pupa	Czizek, 1913:104.
Tipula simplex	General	Doane, 1908.
Tipula subnodicornis	Larva, pupa	Beling, 1886:185–186.
Tipula truncorum	Larva, pupa	Beling, 1879:24–25.

[7] *Tipula micans* is considered by Kertész and others as a synonym of *T. irrorata*, but Beling's descriptions indicate that he had two distinct species before him.

Tipula truncorum	Larva, pupa	Czizek, 1913: 82.
Tipula unca	Larva, pupa, general	Beling, 1886: 179–181 (as *longicornis*).
Tipula unca	Larva, pupa	Czizek, 1913: 101–102 (as *longicornis*).
Tipula variicornis	Larva, pupa	Beling, 1886: 173–174 (as *annulicornis*).
Tipula variicornis	Larva, pupa	Czizek, 1913: 122–123.
Tipula variipennis	Pupa	Beling, 1873 b: 580–581.
Tipula variipennis	Larva	Beling, 1886: 186.
Tipula variipennis	General	Westhoff, 1879.
Tipula variipennis	Larva	Gerbig, 1913: 131–136.
Tipula variipennis	Larva, pupa	Czizek, 1913: 91–92.
Tipula vernalis	Larva, pupa	Beling, 1879: 25–26.
Tipula vernalis	Larva, pupa	Czizek, 1913: 120.
Tipula vittata	Larva, pupa	Beling, 1886: 186–188.
Tipula vittata	Larva, pupa	Czizek, 1913: 78.
Tipula winnertzii[8]	Larva, pupa	Beling, 1873 b: 585–586; 1886: 188–189.
Tipula winnertzii	Larva, pupa	Czizek, 1913: 84–85.
(Nearctic species)		
Tipula abdominalis	Larva	Malloch, 1915–17 b: 200–201 (as *Tipula* sp. 2).
Tipula arctica	Larva, pupa	Nielsen, 1910: 57–59.
Tipula arctica	Larva, pupa	Alexander, 1919 c: 18c, 19c.
Tipula bicornis	Larva, pupa	Forbes, 1890.
Tipula caloptera	Larva	Needham and Betten, 1901: 575–576 (as *abdominalis*).
Tipula cunctans	Larva, pupa, general	Hyslop, 1910 (as *infuscata*).
Tipula cunctans	Larva, pupa	Malloch, 1915–17 b: 204.
Tipula eluta	Larva, pupa, general	Hart, 1898 [1895]: 212–214.
Tipula eluta	Larva, pupa	Malloch, 1915–17 b: 203.
Tipula serta (?)	Pupa	Malloch, 1915–17 b: 205.
Tipula trivittata	Larva, pupa	Greene, 1909.
Tipula trivittata	Pupa	Malloch, 1915–17 b: 204–205.
Tipula ultima	Pupa, general	Needham, 1903: 280–281 (as *flavicans*).
Tipula ultima	General	Caudell, 1913 (as *flavicans*).
Habromastix cinerascens	General	Skuse, 1890: 95.
Nephrotoma analis	Larva, pupa	Beling, 1886: 172–173.
Nephrotoma analis	Larva, pupa	Czizek, 1911: 70–71.
Nephrotoma cornicina	Larva, pupa	Beling, 1879: 39–40 (as *iridicolor*).
Nephrotoma cornicina	Larva, pupa	Czizek, 1911: 76.
Nephrotoma crocata	Larva, pupa	Beling, 1879: 40–41.
Nephrotoma crocata	Larva, pupa	Czizek, 1911: 87.
Nephrotoma lineata	Larva, pupa	Beling, 1879: 42–43 (as *histrio*).
Nephrotoma lineata	Larva, pupa	Czizek, 1911: 83–84.
Nephrotoma lunulicornis	Larva, pupa	Beling, 1879: 41–42.
Nephrotoma lunulicornis	Larva, pupa	Czizek, 1911: 61.
Nephrotoma maculata	Larva, pupa	Beling, 1879: 36–37.
Nephrotoma maculata	Larva, pupa	Czizek, 1911: 80–81.
Nephrotoma pratensis	Larva, pupa	Beling, 1886: 175–176.

[8] Riedel (1913: 25) considers *Tipula winnertzii* as a synonym of *T. truncorum*, but Beling's descriptions indicate that the larvae he had before him represented two distinct species.

Nephrotoma pratensis	Larva, pupa	Czizek, 1911:85–86.
Nephrotoma quadrifaria	Larva, pupa	Beling, 1879:37–39.
Nephrotoma quadrifaria	Larva, pupa	Czizek, 1911:66.
Nephrotoma ferruginea	Larva, pupa	Hart, 1898 [1895]:218–219.
Nephrotoma ferruginea	Larva, pupa	Malloch, 1915–17 b:206.

Tribe **Tipulini**

Subtribe **Dolichopezaria**

Genus **Dolichopeza** Curtis (Gr. *long + feet*)

1825 *Dolichopeza* Curt. Brit. Ent., p. 62.
1830 *Leptina* Meig. Syst. Beschr. Zweifl. Ins., vol. 6, pl. 65, fig. 10.
1846 *Apeilesis* Macq. Dipt. Exot., Suppl. 1, p. 8.

The genus Dolichopeza is a small group of flies including about a score of species, most numerous in the Oriental and Australian regions. The immature stages of the European *Dolichopeza albipes* Ström, a species that is very close to the American species *D. americana* Needm., have been described by Beling (1879, 1886). He found larvae in and beneath moss cushions covering the piles of waste copper slag in the Harz Mountains. On June 11, 1878, larval and pupal material was taken from a tussock of the Jungermanniales liverwort *Alicularia scalaris* Corda. The pupal period was found to be six days. Females were noted depositing their eggs in these hummocks, and small swarms of males were observed dancing near by. It appears that the larvae feed on the upper side of the moss cushion at night, withdrawing into the interior at other times. A larva was found in earth, which shows that these larvae are not dependent on mosses.

The larva is described by Beling (1886:189–191) as being about 12 millimeters long and 2.3 millimeters in diameter. The body is almost terete. The color is a rather bright green, the dorsum being marked with two zigzag dark brown stripes. The spiracular disk has but five lobes; the three dorsal lobes are long and narrow, the median tooth being formed by the apparent fusion of two teeth; the ventral lobes are very short, are tuberculate, and have a small, dark brown, triangular mark at the inner tip. There is a small dark cross-stripe at the base of each lateral lobe. The spiracles are small, are circular, and are separated by a distance equal to about one and one-half the diameter of one. Beneath each spiracle is a rather large, irregular, blackish brown spot. The anal gills are strongly protuberant. The pupa measures about 14.5 millimeters in length and 2.5 millimeters in diameter. The pronotal breathing horns

are directed straight outward and finally downward. The eighth segment has a circle of four dorsal, four ventral, and two pleural spines, which are finely bifid at their tips. The pupa is green, as is the larva, with similar angular dorsal stripes.

This is the only tipuline larva known to the writer with five lobes surrounding the spiracular disk. This feature is the more remarkable when this larva is compared with that of Oropeza, apparently closely related but with a normal tipuline appearance. The immature stages of other species of Dolichopeza and related genera will be of interest.

The resting positions of Dolichopeza are described on page 713 of this paper, and the striking dissimilarities to Oropeza noted. It may be that Oropeza is not so close to Dolichopeza as has been believed. Osten Sacken (1886:157) describes the mating of a European Dolichopeza, presumably *D. albipes,* as follows:

> I had occasion to observe the copula (in Heidelberg, July 26); the female was hanging down from some support to which it held on by its front legs; it bore the whole weight of the male, who was fastened to it merely by the forceps, hanging head downwards, with his legs stretched out. I have seen Bittacomorpha copulate in the same manner.

Genus **Oropeza** Needham (Gr. *mountain + feet*)

1908 *Oropeza* Needm. 23d Rept. N. Y. State Ent. (1907), p. 211.

Larva.— Form somewhat depressed. A strong tubercle on sides of body before spiracular disk. Spiracular disk surrounded by six lobes, the four dorsal ones slender, the ventral pair blunt. Anal gills blunt. Head capsule of the tipuline type. Mandible blunt, with about seven teeth. Hypopharynx five-toothed. Mentum seven-toothed. Coloration dark green.

Pupa.— Pronotal breathing horns elongate-cylindrical, slender. Mesonotum with a slightly elevated triangular area on either side of mid-dorsal line. Leg sheaths ending about on a level, or fore legs a little longer. Abdominal segments with two stout pleural spines; posterior annuli before margin with a transverse row of twelve or fewer spines.

Oropeza is a genus of crane-flies including ten described species, all of which occur in eastern North America with the exception of three Japanese forms. The flies are common beneath dark culverts and bridges, in outhouses, in crannies and crevices of rocky cliffs, beneath overhanging boulders along mountain streams, and in similar situations. The resting positions of the adult flies are discussed on page 712. Many species show a notable predilection for resting on spiders' webs. The immature stages of *Oropeza obscura* are spent in dry moss, as discussed below. Other species have been reared in sandy soil and in wet moss.

Oropeza obscura Johns.

1909 *Oropeza obscura* Johns. Proc. Boston Soc. Nat. Hist., vol. 34, p. 122.

Mr. Hyslop has sent to the writer, at various times during the past two or three years, larvae of *Oropeza obscura.* Numerous larvae and one pupal skin were found under dry moss (*Hedwigia albicans* [Web.] Lindb.) on rocks in the South Mountains, Maryland, on November 4, 1916, by H. L. Parker. They were associated with the larvae of a dascillid beetle, *Eurypogon niger* (Melsh.). Additional specimens were found in a decaying log, but the preferred habitat seems to be beneath moss. The dark green larvae are very sluggish.

Larva.— Length, 11–12 mm.
Diameter, 1.7–1.8 mm.

Color dark brownish green, ventral surface clearer green.

Form depressed; body short and stout. Dorsum covered with small, blackened points, producing the dark color of this region of the body. Segments much wrinkled, especially on basal ring. On each side of penultimate segment a stout tubercle which simulates dorsal lobes of spiracular disk. Spiracular disk (Plate LXXXVI, 469) moderate in size, surrounded by six fleshy lobes, dorsal pair short and slender, lateral pair long and slender, ventral pair very short and blunt; ventral lobes sparsely fringed with short, black hairs, and with a pale apical area bearing a sensory bristle; inner face broadly suffused with brown; at base of other lobes similar but smaller triangular brown marks; a dusky area ventrad of spiracles. Spiracles large, placed obliquely. Anal gills four, large and blunt, pale yellow.

Head capsule of the massive tipuline type. Labrum broad, with a short, blunt lobe on either side; median epipharyngeal region with dense rows of stout setae and two small papillae on margin; lateral lobes with about four or five sensory bristles or papillae of various sizes. Mentum (Plate LXXXVI, 467) seven-toothed, median point long and slender, a prolongation of outer mental plate. Hypopharynx (Plate LXXXVI, 468) five-toothed, the three intermediate teeth the largest, lateral tooth on either side small. Antenna slender, cylindrical, with apical segment very reduced. Mandible rather slender, with about seven blunt teeth on margin. Maxilla with cardo large, triangular, with two setiferous punctures, the outermost very large and hyaline and with two long, powerful setae; lobes of maxilla fringed with dense hairs; palpus short, disklike, with a large group of tiny hyaline papillae at apex.

Pupa.— Length of cast skin, about 12 mm.

Coloration brown; pronotal breathing horns dark blackish brown. (It is possible that the pupae when alive are dark green in color, like the larvae.)

Labrum triangular. Labial lobes large, separated by apex of labrum. Sheaths of maxillary palpi short and stout, apex recurved to beyond midlength. Antennal sheaths moderately elongated. Pronotal breathing horns elongate, slender, cylindrical, tips a little expanded. Mesonotum on either side of median line with a large, roughly triangular, reticulated area which is slightly elevated, with apex of triangle directed toward mid-dorsal line. Mesonotum

transversely wrinkled. Metanotum (Plate LXXXVI, 470) near anterior margin with a transverse row of setiferous punctures, there being four on either side, the intermediate ones with two setae. Wing sheaths reaching base of third abdominal segment. Leg sheaths reaching beyond midlength of fourth abdominal segment, fore legs a little the longest, hind legs a little the shortest.

First abdominal segment on dorsum somewhat similar to metanotum, with a transverse row of four punctures at about midlength, the lateral ones with two setae; remaining abdominal segments (Plate LXXXVI, 471) subdivided into approximately equal basal and posterior rings; on tergites, posterior ring with a transverse row of spines, basal ring unarmed; on sixth tergite, where best developed, spines on posterior ring numbering about twelve, with a seta at each end of the row and two others interspersed; on anterior tergites, spines very small; on seventh tergite spines large, elongated; on eighth tergite four powerful spines in transverse alinement; on pleurites, a strong spine on each ring, that of basal ring deeply bifid and with a strong seta in notch thus formed; posterior ring with a single spine bearing a long seta on its face; on sternites, condition generally similar to that on tergites, the spines a little more prominent but of about the same number, these spines slender at their slightly curved tips and lacking on sternites 2 to 4. Female cauda (Plate LXXXVI, 472 and 473) with acidothecae elongate, contiguous, on either side of tergites at base with a powerful incurved hook; posterior margin of eighth tergite with four spines, lateral pair a little the larger; ventral side at base with a median protuberance bearing two powerful lateral lobes and two smaller chitinized spines which are directed caudad and ventrad; base of segment 8 with a crossrow of eight spines; posterior ring of segment 8 with a powerful spine at lateral end.

Nepionotype.— South Mountains, near Myersville, Maryland, March 31, 1916.
Neanotype.— Hagerstown, Maryland, May 9, 1916; cast pupal skin in collection of United States National Museum.
Paratypes.— Larvae from type locality.

Genus **Brachypremna** Osten Sacken (Gr. *short* + *trunk*)

1886 *Brachypremna* O. S. Berl. Ent. Ztschr., vol. 30, p. 161.

Larva.— Unknown.

Pupa.— Antennal segments enlarged at base. Antenna short. Sheaths of maxillary palpi short, not recurved at tips. Pronotal breathing horns short, slender, finely annulated. Mesonotum with eight prominent tubercles. Leg sheaths reaching beyond midlength of fourth abdominal segment, fore tarsi very short, other tarsi subequal in length. Abdominal segments each with four slender spines on posterior ring of both sternites and tergites, just before posterior margin; two pleural spines; eighth segment of male with four prominent, spinous lobes.

Brachypremna is a small genus, including but nine recent species found in the Austral and Tropical regions of the New World. *Brachypremna eocenica* Meunier is described from the Baltic amber. The flies of the best-known species, *B. dispellens,* are known in parts of the Southern

States as "weavers." They frequent rather shady places and have a remarkable dance over three or four feet of vertical space, whence the name "king of the dancing tipulids" given them by Johnson. This species is the only one whose immature stages are at all known.

Brachypremna dispellens (Walk.)

1860 *Tipula dispellens* Walk. Trans. Ent. Soc. London, n. ser., vol. 5, p. 333–334.
1886 *Brachypremna dispellens* O. S. Berl. Ent. Ztschr., vol. 30, p. 162.

Brachypremna dispellens is the most widely distributed species of the genus. It ranges from New Jersey southward thru North America, and thru South America as far as Argentina. A larva found by R. C. Shannon in a rotten log by a stream near Washington, D. C., on April 23, 1913, was placed in rearing and emerged in May as an adult male of this species. The badly mutilated pupal skin was preserved and is here described. No part of the larva was preserved.

Pupa.— Length of cast pupal skin, about 18 mm.

Coloration brownish yellow; abdomen with a broad brown sublateral stripe on both ventral and dorsal segments; each of pleural spines set in a brown spot.

Head small. Antennal spines very large and crowded at base, soon passing into the short, slender flagellum. Labrum (Plate LXXXVII, 474) blunt. Labial lobes closely approximated, so as to appear as a single large, transversely rectangular lobe at end of labrum. Sheaths of maxillary palpi short, not recurved at tip. Pronotal breathing horn (Plate LXXXVII, 475) small, slender, curved, ringed with fine annuli, tapering gradually to the small apex; margin of apex set with breathing pores. Mesonotum with eight conspicuous, blunt, naked tubercles; the four intermediate tubercles larger, arranged in the form of a trapezoid; anterior median pair high, conical, located rather close to mid-dorsal line. Wing sheaths reaching end of second abdominal segment. Leg sheaths (Plate LXXXVII, 476) extending beyond mid-length of fourth abdominal segment; fore legs very short, ending opposite base of third tarsal segment of other legs.

Abdominal tergite 1 with a pair of long, slender spines before posterior margin; segments 2 to 7 subdivided into a basal and a posterior ring, the latter with a transverse row of four long, slender spines before posterior margin, the seventh tergite with about six such spines; sternites similar, with four spines on posterior ring; pleurites with a slender spine on basal and posterior ring; at base of posterior ring between spines, an indistinct, slightly protuberant spiracle. Male cauda (Plate LXXXVII, 477) narrowed, small, valves blunt; on dorsal side near base four conspicuous lobes, each terminating in a slender, chitinized spine; a small acute spine on sides of ninth segment at base.

Neanotype.— Cast pupal skin, Washington, D. C., May, 1913 (in collection of United States National Museum).

Subtribe **Ctenophoraria**

Genus **Ctenophora** Meigen (Gr. *comb* + *to bear*)

1800 *Flabellifera* Meig. Nouv. Class. Mouch., p. 13 (*nomen nudum*).
1803 *Ctenophora* Meig. Illiger's Mag., vol. 2, p. 263.
1910 *Phoroctenia* Coq. Proc. U. S. Nat. Mus., vol. 37, p. 589.

Larva.— Body opaque, integument rather thick. Spiracular disk surrounded by six lobes.

Pupa.— Sheaths of maxillary palpi recurved. Pronotal breathing horns long and slender Two spines on mesonotum. Fore and middle tarsi subequal, a little shorter than hind tarsi. Ventral abdominal segments with six to eight spines.

Ctenophora is a small genus including about sixteen nominal species found thruout the Holarctic region. The larvae and the pupae occur in decaying wood. The early stages have long been known, having been described by Réaumur and De Geer.

In Europe, *Ctenophora flaveolata* (Fabr.) is described and figured by Réaumur (1740) and by Weyenbergh (1872). *C. pectinicornis* (Linn.) is described or mentioned by Bouché (1834), by Fischer von Waldheim (1838), by Zetterstedt (1851:4014), by Weyenbergh (1872), and by Kaltenbach (1874). *C. festiva* Meig. was reared by Kaltenbach (1874:631) from larvae in decayed beech stems. *C. nigricoxa* Lundst. (*Malpighia vittata* Meig., auct. Frey) was reared by Lundström (1906:7) from pupae in rotten birch stumps. The immature stages of the various European species of Ctenophora are described as living in the wood of various trees such as willow (Salix), birch (Betula), cherry (Prunus), and other hardwood species.

In North America, *C. apicata* is described by Johannsen (1910) from elm (Ulmus), and *C. angustipennis* Loew by Anthon (1908) in alder (Alnus) and in poplar (Populus). The latter species is recorded also as injuring prune trees (Prunus) in Oregon, by Lovett (1915), who gives an excellent account of all stages and the type of injury done. The female lays from 200 to 400 eggs, which hatch in from nine to seventeen days and the larvae tunnel into the surrounding dead wood. Here they feed and grow, reaching maturity the following spring. Pupation takes place in the burrows, the pupal stage requiring about ten days. Osten Sacken (1877:211) supposed that the larvae live in the stumps of redwood (Sequoia), but this has never been confirmed.

Ctenophora apicata O. S.

1864 *Ctenophora apicata* O. S. Proc. Ent. Soc. Phila., vol. 3, p. 46.

The larvae and the pupae of *Ctenophora apicata* that were described by Johannsen (1910) have been studied by the writer in the collection of the Maine Agricultural Experiment Station. They were collected at Orono, Maine, on June 23, 1909, by Dr. William C. Woods. In 1913 the writer examined the stump from which they were taken, and found a few cast pupal skins.

The notes here given are taken partly from Dr. Johannsen's description and partly from the original material.

Larva.— Length, about 30 mm.

Color white. Body stout, cylindrical. Antenna cylindrical, with an apical papilla. On dorsum of head behind antennae, a slender, flexible spine. Spiracular disk surrounded by six lobes, dorsal and lateral pairs slender, finger-like; ventral pair blunt.

Pupa.— Length, 25–27 mm.
Length of breathing horns, 3 mm. additional.
Width, d.-s., 5.2 mm.
Depth, d.-v., 5 mm.

Pupa somewhat similar to that of Tanyptera, differing as follows: Form stout; abdomen a little depressed. Sheaths of maxillary palpi strongly recurved at tips. Pronotal breathing horns long and slender. Mesonotum with a prominent tuberculate spine on either side of median line. Legs short, ending before tip of third abdominal segment; tarsal sheaths ending about on a level, or those of hind legs a very little longer. Abdominal segments 5 to 7 with six to eight spines. Female cauda with six powerful ventral spines or tubercles and two dorsal tubercles on either side. Valves of ovipositor short, tergal valves a little longer than sternal valves.

Nepionotype.— Orono, Maine, July, 1909.
Neanotype.— Orono, Maine, July, 1909.
Paratypes.— Numerous pupae in collection of Maine Agricultural Experiment Station.

Genus **Dictenidia** Brullé (Gr. *double + comb*)

1833 *Dictenidia* Brullé. Ann. Soc. Ent. France, vol. 2, p. 401–402.
1856 *Ceroctena* Rond. Dipt. Ital. Prodr., vol. 1, p. 186.
1863 *Dicera* Lioy. Atti dell' Institut Veneto, ser. 3, vol. 9, p. 216.

Dictenidia is a genus of Palaearctic crane-flies including three species, of which one is European and the others are Japanese. The genotype, *Dictenidia bimaculata* Brullé, is very well known. The immature stages are described or mentioned by Bouché (1834), by Zetterstedt (1851), by Weyenbergh (1872), by Beling (1873 b), by Czizek (1913), and by other investigators. Beling found the larvae in decaying birch (Betula). He describes the larvae as being grayish yellow, with four spiracular lobes. The pupal duration is seven days. Osten Sacken (1886: 173–175) states that he has often found larvae in the wet detritus underneath the bark

of decaying trees. The larvae are much closer to Ctenophora than to Tanyptera, the skin being tough and opaque, with a fine pubescence, and the spiracular disk consisting of small but distinct lobes. The pupae likewise are similar to those of Ctenophora, having the pronotal breathing horns elongate, five spines on abdominal sternites 3 to 6, and four spines on tergites 2 to 7.

Genus **Tanyptera** Latreille (Gr. *extend* + *wing*)

1805 *Tanyptera* Latr. Hist. Nat. Crust. et Ins., vol. 14, p. 286.
1832 *Xiphura* Brullé. Ann. Soc. Ent. France, vol. 1, p. 206.

Larva.— Integument very thin, with numerous setae, those on dorsum very small. Spiracular disk with lobes practically lacking. Spiracles large, lying exposed on the face of last segment. Anal gills bluntly rounded. Mandible small, with one dorsal and one ventral tooth. Antenna cylindrical, capped with an apical cone. Mentum with seven to nine teeth.

Pupa.— Cephalic crest lacking. Sheaths of maxillary palpi not recurved at tips. Pronotal breathing horns large, broadly flattened, margin deeply crenulated. Mesonotum with two blunt tubercles. Abdominal segments with six to ten spines on tergites, three to five spines on sternites.

Tanyptera is a small genus including about twelve nominal species whose limits and relationships are still but little understood. The immature stages are spent in the decayed or partly decayed wood of various deciduous trees.

In Europe, *Tanyptera atrata* (Linn.), the genotype, was found by Perris (1840) and by De Rossi (1882) in decaying alder (Alnus) stems. Nördlinger (1848) found the same species in linden (Tilia) and in poplar (Populus). It has also been taken in oak (Quercus), beech (Fagus), birch (Betula), and other hardwood species. Gerbig (1913) discussed the variety *ruficornis* Meig. under the name *Ctenophora flavicornis*.

In America, Malloch (1915–17 b: 194–195) describes *T. fumipennis* (O. S.) from a much-decayed chestnut log (Castanea), and later (1919) in basswood (Tilia), where the species was associated with larvae of *Xylota fraudulosa* Loew and *Chalcomyia aerea* (Loew), of the family Syrphidae. *Tanyptera frontalis*, discussed below, was found in red maple (Acer).

Tanyptera frontalis (O. S.)

1864 *Ctenophora frontalis* O. S. Proc. Ent. Soc. Phila, vol. 3, p. 48.

The writer found numerous larvae of *Tanyptera frontalis* in a fallen log of red maple (*Acer rubrum* Linn.) near Beebe Lake, Ithaca, New York, on March 22, 1913. Larvae of several sizes were found. They were working in wood which was well preserved, not entirely sound but still so hard that it had to be cut with a hatchet. The larvae pupated in April. A small male emerged on May 1.

Other larvae of Tanyptera were found in a hickory log (*Carya* sp.) at Sandy Landing, Virginia (opposite Plummers Island), on September 9, 1913. Detailed drawings of the larval structure made by Dr. Böving are in the collection of the United States National Museum.

Larva.— Length, 30–35 mm.
Diameter, 7–7.2 mm.

Coloration, pale yellowish white.

Form terete, very stout. Integument thin. Numerous long black setae on segments (Plate LXXXVIII, 482), arranged in transverse rows before posterior margin; setae of dorsum (Plate LXXXVIII, 481) very tiny, one on either side of median line; a pair of setae laterad of these and in alinement; setae on pleural region very long and delicate; on thoracic segments, setae at about midlength; on abdominal segments, setae closer to posterior margin; mid-ventral setae very tiny, four in number, on thoracic segments at about midlength, forming a stiff pencil on sides of venter, with two small setae between; laterad of these four intermediate setae, a group of three setae, two long and one very short; ventral setae lying at a level posterior to that of pleural setae. Spiracular disk (Plate LXXXVIII, 483) with lobes practically lacking, the two large, oval spiracles lying exposed on truncated end of last segment; above and laterad of each spiracle, a small, blunt lobe with a blackened mark and three long setae; below spiracles, two narrow black lines representing the two ventral lobes; a small pencil of setae below each of these marks, and each mark having a sensory bristle; three or four long setae on sides of spiracular disk. Spiracles with small middle piece black, ring yellowish brown; spiracles separated by a distance a little greater than diameter of one. Anal gills four, bluntly rounded, very protuberant and evidently formed for propulsion. (In older specimens the anal gills are minutely roughened and are darker in color.)

Head capsule of the massive tipuline type. Labrum rather broad; median epipharyngeal region with a small brush of hairs surrounding two sensory setae; lateral lobes large, on their ventral face densely hairy, surrounding four sensory setae and a flattened hyaline peg. Mentum (Plate LXXXVIII, 478) rather small, broadly rounded, anterior margin with seven or nine teeth, in the latter case the outermost tooth on either side very blunt and reduced, the median tooth long and flattened. Antenna (Plate LXXXVIII, 479) short-cylindrical; apical papilla very small, hyaline, conical, with surface sculptured; in addition to this cone, three or four small hyaline sense pegs; the usual auditory organ located at about midlength of segment. Mandible (Plate LXXXVIII, 480) small, with one dorsal and one ventral tooth in addition to the apical point, ventral tooth flattened and with margin crenulated; a stout seta at heel of mandible; prostheca an elongated cone, situated at base

of mandible. Maxilla rather small, simple; palpus large, antenniform, with apex bluntly rounded; inner lobe densely covered with short, stout setae surrounding a powerful bristle and a small brown sensory organ.

Pupa.— Length, 30–33 mm.
Width, d.-s., 5–6 mm.
Depth, d.-v., 5.5 mm.

Coloration pale yellow; pronotal breathing horns liver-colored. (In older specimens, the thorax and appendages are dark-colored, and the abdomen has broad brown sublateral stripes.)

Head rather small, cephalic crest lacking. Antenna stout, rather elongate, extending far beyond ends o palpi, segments angulated. Clypeus and labrum tumid, transversely wrinkled. Labial lobes slender, divergent. Sheaths of maxillary palpi rather slender, tips curved but not recurved (Plate LXXXVIII, 485). Pronotal breathing horn (Plate LXXXVIII, 486) large, broadly flattened, slightly incurved, broader at apex than at base, deeply furrowed up middle of outer face, the broad margin thus formed deeply wrinkled to crenulate. Mesonotum large, transversely wrinkled, with two blunt tubercles provided with short setae (Plate LXXXVIII, 484). Wing sheaths small, reaching end of second abdominal segment. Leg sheaths ending before tip of third abdominal segment; fore tarsi very short, hind tarsi the longest, those of middle legs intermediate.

First abdominal tergite with two spines; segments 2 to 7 broad, divided into the usual basal and posterior rings; second segment on posterior ring with four spines; segments 3 to 6 with six to ten spines, the intermediate ones usually smaller; segment 7 with four spines; pleurites with a spine on each ring; sternites with similar arrangement to that of tergites, but spines usually fewer in number, segments 3 and 4 with only a single widely separated spine on each side, segments 5 and 6 with four or five spines, segment 7 with three spines; segment 8 has four small spines between the large lateral ones described below. Male cauda blunt, dorsal lobes very divergent, ending in sharp, chitinized points. Female cauda (Plate LXXXVIII, 487) with tergal valves elongate, narrowed to the moderately acute tips; sternal valves similar in shape but smaller; lateral lobes of ninth segment directed caudad and laterad, at tips running out into chitinized points; two small setae before tips; segment 8 with a powerful lateral lobe on either side, each terminating in a chitinized point; posterior lateral angles of segment produced into slender, blunt points.

Nepionotype.— Ithaca, New York, March 22, 1913.
Neanotype.— May 1, 1913. No. 11-1913.
Paratypes.— Four larvae and two pupae with types.

Subtribe **Tipularia**

Genus **Longurio** Loew (Lat. *a tall man*)

1869 *Longurio* Loew. Berl. Ent. Ztschr., vol. 13, p. 2.

Larva (supposition).— Body massive. Integument semi-transparent. Form clearly depressed. Spiracular disk surrounded by six lobes, dorsal pair very small, ventral pair very long; ventral and lateral lobes provided with but few setae at and near tips; spiracular

disk and lobes unmarked. Spiracles small. Anal gills branched. Mandible small, with but a single dorsal and ventral tooth in addition to apical point. Mentum with nine teeth. Hypopharynx five-toothed.

Pupa.— Antenna short, ending opposite tips of maxillary palpi. Sheaths of maxillary palpi not recurved at tips. Mesonotum unarmed. Pronotal breathing horns very long and slender, one, at least, about half length of body. Wings showing clearly the characteristic venation of Longurio. Abdomen elongate, posterior ring of individual segments with short, stout spines, including a few on pleurites; dorsum of eighth segment with four powerful lobes.

Longurio is a small genus including about ten described species, of which two occur in eastern North America. The genotype, *Longurio testaceus,* is the best-known species locally. The immature stages of this species are here discussed for the first time. They are spent in sand or sandy earth. The branched anal gills of the larva, and the excessively elongate breathing horns of the pupa, are notable features.

Longurio testaceus Loew

1869 *Longurio testaceus* Loew. Berl. Ent. Ztschr., vol. 13, p. 2.

Longurio testaceus is probably the largest crane-fly in North America, the females exceeding the better-known Holorusia of the Western States. The adult flies are difficult to capture, being very wary. When the insect is at rest the body generally hangs perpendicularly, with the wings folded incumbent over the abdomen.

On November 9, 1916, Mr. Hyslop sent the writer two living larvae which are referred with little doubt to this species. They were found in wet sand in a bog on the top of South Mountains, near Myersville, Maryland. The larvae were very restless, the head capsule being constantly exserted and withdrawn. Waves of contraction start from the posterior end of the body and pass toward the head. A large pupa taken by Dr. J. C. Bradley at Tallulah Falls, Georgia, on June 17, 1910, undoubtedly belongs to this species, the venation being clearly apparent on the wing pad. An additional cast pupal skin is in the collection of the United States National Museum.

Larva (supposition).— Length, 31 mm. contracted, 58 mm. extended.
Diameter, 11–12.5 mm.

Color whitish, subhyaline; thoracic segments more yellowish; in life the brown food contents showing clearly thru abdomen.

Form very depressed, lateral folds prominent; body very stout and fleshy. Skin very thin and semitransparent, showing internal organs within, practically destitute of pubescence;

a few short setae on body, especially on thoracic segments. Spiracular disk (Plate LXXXIX, 490) large, flattened, surrounded by six lobes; dorsal pair very small, represented by two short, conical protuberances; lateral and ventral lobes slender, the latter a little the longer, each with three or four long, delicate setae at tip and two or three others before tip on outer face; a long seta on margin of disk between dorsal and lateral lobes; spiracular disk and lobes entirely unmarked with darker. Spiracles small, circular, stigmal rings very narrow; spiracles separated by a distance equal to about three times diameter of one. Anal gills four, large, pinnately branched, each gill with six lateral branches.

Head capsule massive, of the tipuline type. Labrum with a distinct, densely hairy lobe on either side. Mentum (Plate LXXXIX, 488) large; anterior margin with nine slender teeth, median one the longest, outermost teeth on either side blunt, flattened, evidently formed by fusion of two teeth. Hypopharynx (Plate LXXXIX, 489) five-toothed; teeth blunt, the three middle ones larger, the lateral tooth on either side a little smaller. Antenna long and slender, cylindrical; apex blunt and without distinct sense pegs or setae. Mandible small, with a large conical dorsal tooth and a single flattened ventral tooth in addition to apical point; prostheca distinct. Maxilla small; palpi large, cylindrical, truncated at apex and with a circular auditory plate near end; inner lobe of maxilla with abundant elongate setae.

Pupa.— Length, 42–45 mm.
Length of longest breathing horn, 18–19 mm. additional.
Width, d.-s., 3 mm.
Depth, d.-v., 4.2 mm.

Color dark brown; pronotal breathing horns paler at tips; mesonotum chestnut brown; abdominal segments indistinctly ringed with pale and darker.

Front between antennal bases swollen, finely tuberculate but without distinct setae. Antenna very short, ending opposite tips of maxillary palpi. Labrum large. Sheaths of maxillary palpi not recurved at tips. Mesonotum unarmed, with fine transverse wrinkles. Pronotal breathing horns (Plate LXXXIX, 491) very long and slender, the right one, at least, exceedingly elongate, with tip expanded. (The left breathing horn was broken before the apex in both the pupae studied; it was almost as long as the right horn, and may, of course, have been longer.) Wing pads reaching end of second abdominal segment; characteristic venation of genus showing clearly on sheath. Leg sheaths long, extending to beyond midlength of fourth abdominal segment; fore legs shorter than the others.

Abdomen elongate. Abdominal segments 2 to 7 near posterior margin with a transverse row of short, stout spines which are interrupted only near pleura; pleural area with four or five spines; ventral and dorsal segments with numerous spines; dorsal row of spines more distant from posterior margin of segment than the other areas; dorsum of eighth segment with four powerful, chitinized lobes directed dorsad and caudad; posterior margin of these lobes with about five or six small teeth; two spines near base of pleural region on segment 8. Male cauda consisting of two blunt sheaths, lying between posterior pair of lobes described above.

Larva.— South Mountains, near Myersville, Maryland, November 6, 1916.
Neanotype.— Tallulah Falls, Georgia, June 17, 1910.
Paratype.— Cabin John Bridge, Maryland, May 31, 1900.

Genus **Aeshnasoma** Johnson (Gr. *a dragon fly + body*)

1909 *Aeshnasoma* Johns. Proc. Bost. Soc. Nat. Hist., vol. 34, p. 115–116.

Aeshnasoma is a monotypic genus found in northeastern North America. It is unquestionably close to Longurio and may be congenerous with it. The type, *Aeshnasoma rivertonensis* Johns., is apparently very local in its distribution.

Johnson (1906:1–2) described an unknown tipuline larva which undoubtedly pertains to this species. The larva was found on June 10, 1900, in a cold spring at Riverton, New Jersey. It was brought into the laboratory but could not be reared, the change from the cold spring (about 60° F.) to warmer waters being fatal. The larva when fully extended measured about 45 millimeters in length. It was yellowish white in color and was translucent, the alimentary canal with its contents being clearly visible thru the thin skin. Johnson describes and figures the peculiar branched anal gills (Plate LXXXIX, 492) of this genus. The larva was doubtfully referred to Longurio, the adults of Aeshnasoma being undescribed at that time.

In a later paper (1907–12 [1909]:115–116) Johnson mentions the taking of several more larvae in 1902, and, on July 20, the capture of the adult flies on which the genus and species are based.

The only larva that was preserved was kindly sent to the writer for study by Mr. Johnson. It is undoubtedly very close to Longurio, both genera showing the same peculiar spiracular disk and the branched anal gills, a condition that is found nowhere else in the Tipulidae so far as is known to the writer.

Genus **Holorusia** Loew (derivation obscure)

1863 *Holorusia* Loew. Berl. Ent. Ztschr., vol. 7, p. 1.

Larva. — Spiracular disk surrounded by six moderately elongate lobes fringed with long hairs; inner face of lateral and ventral lobes with capillary black lines; disk between spiracles dusky. Anal gills six. Mandible small, with a single dorsal and ventral tooth in addition to apical point. Antenna with a conical apical papilla. Mentum seven-toothed. Hypopharynx six-toothed.

Pupa. — Sheaths of maxillary palpi recurved at tips. Pronotal breathing horns rather short and stout, the long apices flattened. Armature of abdominal segments almost as in Prionocera, but the posterior rows of spines more numerous (fourteen to twenty-four); pleurites with three spines, the two on posterior ring situated one behind the other. Cauda with six stout dorsal lobes.

Holorusia is a small genus (about ten species) of New World crane-flies, only one of which—the genotype, *Holorusia rubiginosa* — is Nearctic. This species and Longurio are the largest Nearctic crane-flies. The anatomy of the "giant crane-fly" has been described in some detail by Kellogg (1901, a and b) and by Comstock and Kellogg (1904). The immature stages are spent in moist earth. The genus is undoubtedly closely related to Prionocera, and, presumably, to the Old World genus Ctenacroscelis Enderlein.

Holorusia rubiginosa Loew

1863 *Holorusia rubiginosa* Loew. Berl. Ent. Ztschr., vol. 7, p. 1.
1888 *Tipula (Holorusia) grandis* Bergr. Ent. Tidskr., vol. 9, p. 140.

Holorusia rubiginosa is widely distributed thruout the western United States and Canada. A number of larvae were taken by H. Morrison near Stanford University, California, on February 22, 1915. They were shipped to the writer at Ithaca, New York, where the species was reared. The massive larva is used for purposes of dissection in the entomological courses at some of the western universities.

Larva.— Length, 50–60 mm.
Diameter, 6.2–6.4 mm.

Coloration, dark greenish brown.

Form stout, subterete. Integument covered with dense, short, erect, black hairs. A few weak and delicate setae, two on dorsum and on venter of each abdominal segment; two long setae on lateral margins of posterior rings. Spiracular disk (Plate XC, 496) moderately large, surrounded by six stout, elongate lobes which are similar to those of Prionocera but are stouter and less digitiform; ventral lobes a little the longest, dorsal lobes a little the shortest; all the lobes capable of close approximation, completely protecting spiracles; lobes fringed with long black hairs which are longest near apices, shorter between lobes; ventral and lateral lobes with a delicate black line down inner face, these lines barely indicated on dorsal lobes; remainder of disk and lobes dusky. Spiracles very large, circular, separated by a distance a little less than diameter of one. Anal gills six, short, slender, the two anterior gills of either side united basally, posterior pair simple.

Head capsule of the usual massive tipuline type, prefrons running caudad as a narrow point, lateral plates broad. Labrum broad, with a densely hairy lobe on either side. Mentum (Plate XC, 493) with a prominent median point; behind it on either side three flattened teeth, the innermost the broadest, the middle tooth more acute, the outermost formed by fusion of two small teeth. Hypopharynx (Plate XC, 494) about six-toothed, the intermediate teeth with a large notch between. Antenna (Plate XC, 495) with basal segment very long and slender; principal apical papilla conical; a number of small hyaline sense pegs. Mandi-

le slender, with only two teeth, a stout dorsal tooth and a single flattened ventral tooth. Iaxilla small, lobes covered with short, dense hairs.

Pupa.— Length, 32 mm.
Width, d.-s., 5 mm.
Depth, d.-v., 5 mm.

Color brown; flattened lateral margins of abdomen broadly yellowish.

Thorax terete; abdomen depressed, with lateral margins flattened, carinate. Cephalic rest represented by two low, parallel ridges, provided with one or two tiny setae. Labrum rge, tumid, transversely wrinkled, the blunt apex completely separating the diamond-aped labial lobes. Maxillary palpi stout, extreme tip recurved. Antenna moderately longated, extending some distance beyond maxillary palpi. Pronotal breathing horns rather ort and stout, finely ringed, the rather long tips flattened, about equal to one-fifth length f entire organ. Mesonotum convex (Plate XC, 497), with transverse anastomosing rinkles; on either side of median line behind, a blunt tubercle. Wing sheaths reaching end f second abdominal segment. Leg sheaths extending just beyond base of fourth abdom-al segment; fore tarsi short, middle tarsi a little longer than hind tarsi.

Abdominal segments with the usual basal and posterior rings; armature almost as in Prionocera; tergites with posterior row of spines numbering between twenty and twenty-our on intermediate segments, near anterior lateral angle two spines, basal ring unarmed; leurites with one setiferous spine on basal ring and two similar spines on posterior ring, ne placed considerably behind the other; sternites armed similarly to tergites, but the poste-ior row of spines larger and somewhat fewer in number (fourteen to eighteen); posterior ring n either side median line near base with two spines, the innermost very large and power-ul. Male cauda with ventral lobes blunt, each armed with a slender black spine near pos-erior margin; dorsal surface of cauda almost as in Prionocera, armed with six stout lobes, hich here are shorter and stouter, with tips abruptly narrowed; lateral margin of segment with a stout lobe on either side, each terminating in a cylindrical spine. Female cauda imilar to male cauda, dorsum with the same six lobes; acidothecae short, tergal valves lightly exceeding the more blunt sternal valves.

Nepionotype.— Stanford University, California, February 27, 1915.
Neanotype.— April 5, 1915.
Paratypes.— Larvae and pupae with types.

Genus **Prionocera** Loew (Gr. *saw* + *horn*)

. 1844 *Prionocera* Loew. Stett. Ent. Zeit., vol. 5, p. 170.
1863 *Stygeropis* Loew. Berl. Ent. Ztschr., vol. 7, p. 298.

Larva.— Spiracular disk surrounded by six long, finger-like lobes fringed with long, deli-ate hairs; each lobe with a capillary black line down middle of inner face. Spiracles large. Anal gills unbranched. Mentum seven- to nine-toothed. Hypopharynx five-toothed. Mandible with about two dorsal and three ventral teeth.

Pupa.— Maxillary palpi recurved at tips. Pronotal breathing horns very elongated, nequal, the longer one about half length of body; horns at tips split into long flaps. Abdom-nal tergites with a posterior transverse row of fifteen or fewer spines, and two small spines

near anterior lateral margin of posterior ring; pleurites with a spine on basal ring and two transverse spines on posterior ring. Cauda with six strong dorsal lobes.

Prionocera is a small genus (about a dozen species) of usually far northern flies of somber coloration. The only species found in eastern North America is *Prionocera fuscipennis*, discussed below. The immature stages are somewhat similar to those of Holorusia. The apparent similarity of the pupa to that of Longurio is probably not indicative of a very close relationship.

The immature stages have been discussed but little in the literature. The "Tipula sp. No. 1" of Malloch (1915–17 b: 199–200) refers to *P. fuscipennis.* The immature stages of a species supposed to be *P. parri* (Kirby) have been discussed and figured by the writer in his report on the Canadian-Arctic Tipulidae (Alexander, 1919 c: 19c–20c).

The name *Stygeropis* has been in use for many years under the belief that the earlier name *Prionocera* was preoccupied in the Coleoptera. Dr. Bergroth states that this is not so and that Prionocera should be used.

Prionocera fuscipennis (Loew)

1865 *Stygeropis fuscipennis* Loew. Berl. Ent. Ztschr., vol. 9, p. 129.

C. H. Kennedy found two cast pupal skins among Sparganium stems in Ringwood Hollow, Ithaca, New York, on November 20, 1916. Several larvae had been found here in the preceding July, and some others were found on June 4, 1917 (No. 106–1917), in a cat-tail swamp near Bool's hillside, Ithaca, where they were associated with the characteristic helophytic crane-fly fauna (Bittacomorpha, *Rhamphidia flavipes*, *Pseudolimnophila luteipennis*, *Pilaria recondita*, *Tipula tricolor*, and other species). Malloch's material was taken in Wisconsin in May. Dr. Needham has reared the species near Lake Forest, Illinois.

Larva.— Length, 18–22 mm.
Diameter, 2–2.2 mm.

Coloration dark brown, in some cases with a pale dorso-median stripe.

Form terete, tapering gradually to anterior end of body. Segments with several scattered elongate setae. Spiracular disk (Plate XCI, 502) surrounded by six long, finger-like lobes which are delicately fringed with long hairs; ventral lobes considerably the longest; lateral lobes a little larger and stouter than dorsal lobes; all the lobes broadly margined with dark brown, these marks expanding at inner ends; on ventral lobes, lateral margin expanded at inner

end and continued across disk, meeting its fellow of the opposite side between spiracles; lorsal margin of lateral lobes touching spiracles; each of the lobes marked with a capillary lark brown line down center of inner face, this beginning near ends of lobes and extending almost to base; lobes fringed with long hairs, these very tiny near base, longer near tips of obes, but scarcely, if at all, interrupted between lobes. Spiracles large, circular, sepa-rated by a distance a little greater than diameter of one. Anal gills six, long, slender, unbranched.

Head capsule of the usual tipuline type. Labrum covered with dense, short hairs, those on lateral lobes longer. Mentum (Plate XCI, 498) usually seven-toothed, in some cases nine-toothed; median tooth slender, lateral teeth flattened, subacute. Hypopharynx (Plate XCI, 499) narrow, five-toothed. Antenna (Plate XCI, 500) long and slender; first segment a little enlarged near base; at apex several tiny sensory papillae; auditory plate near base of segment. Mandible (Plate XCI, 501) moderately large, with two large dorsal and about three ventral teeth; prostheca large. Maxilla small; palpus large, cylindrical, apex truncated.

Pupa.— Length, 15–22 mm.
Width, d.-s., 2.4 mm.
Depth, d.-v., 2.6 mm.

Coloration dark brown; lateral and posterior margins of abdominal segments paler. (In old specimens the general coloration is very dark brown; in younger specimens the abdomen is more or less distinctly lined with brown.)

Thorax subterete; abdomen depressed, lateral margins flattened. Labrum broad, apical point narrow. Labial lobes broad, slightly separated on median line. Maxillary palpi short, stout, apex recurved. Antenna moderately elongated, extreme tip darkened. Pronotal breathing horns long and slender, unequal in length, the longer about 9 or 10 mm. in length, the other 6 mm., at tips split into divergent flaps (Plate XCI, 504) almost as in the hexatomine genera Pseudolimnophila and Pilaria, which live in the same muddy situations. Mesonotum (Plate XCI, 503) transversely wrinkled. Leg sheaths reaching posterior margin of third abdominal segment; hind legs the longest; middle legs a little shorter than fore legs.

Abdominal segments divided into a basal and a posterior ring; tergites with basal ring unarmed; posterior ring with a subterminal transverse row of short spines, with a few setae located on lateral face of some of the spines; on second tergite, four to six spines, on tergites 3 to 7, three to fifteen spines; two small spines with setae near anterior lateral angle of posterior ring; pleurites with a small setiferous spine on basal ring, and two such spines on posterior ring located side by side; sternites with the basal ring unarmed, posterior ring armed similarly to that of tergites; in addition to posterior row of spines, a pale oval area on either side of midventral line, each with two transversely placed spines. Male cauda (Plate XCI, 505) with four powerful lobes on dorsum of last segment, directed dorsad and slightly caudad, lobes bearing three or four small spines before tips; between anterior pair of lobes, two additional slender lobes, each ending in two acute spines.

Nepionotype.— Ringwood Hollow, Ithaca, New York, July 20, 1916.
Neanotype.— Cast pupal skin, type locality, November 20, 1916.
Paratypes.— Larvae and pupal skins, type locality.

Genus **Tipula** Linnaeus (Lat. *a water-strider*)

1758 *Tipula* Linn. Syst. Natur., ed. 10, p. 585.
1842 *Pterelachisus* Rond. Mag. Zool. Ins., pl. 106.
1864 *Anomaloptera* Lioy. Atti dell' Institut Veneto, ser. 3, vol. 9, p. 218.
1887 *Oreomyza* Pokorny. Wien. Ent. Ztg., vol. 6, p. 50.
1894 *Manapsis* Scudder. Proc. Amer. Philos. Soc., vol. 32, p. 222.
1894 *Rhadinobrochus* Scudder. Proc. Amer. Philos. Soc., vol. 32, p. 223.
1894 *Tipulidea* Scudder. Proc. Amer. Philos. Soc., vol. 32, p. 238–239.
1916 *Nippotipula* Mats. Thous. Ins. Japan, add. 2, p. 457–458.
1916 *Platytipula* Mats. Thous. Ins. Japan, add. 2, p. 459.
1916 *Yamatotipula* Mats. Thous. Ins. Japan, add. 2, p. 461–462.
1916 *Togotipula* Mats. Thous. Ins. Japan, add. 2, p. 465.

Larva.— Form generally stout, terete or nearly so. Integument with pubescence an almost invariably with a definite chaetotaxy. Spiracular disk surrounded by six or rarel eight lobes, simple, or in certain species (as *T. abdominalis*) more or less split at their tip Spiracles small and widely separated (in *T. abdominalis*), or in other species large and rathe close together. Anal gills almost invariably present, with six or eight branches, thes branches simple, not pinnate. Head capsule compact and massive. Labrum broadly trans verse. Mandible usually small, with few teeth, ventral cutting edge with usually two o three teeth. Maxilla rather complicated, of the generalized tipuline structure. Antenn usually elongated, basal segment two to four times as long as it is thick, stouter in speci living in decaying wood. Mentum with seven to nine teeth. Hypopharynx a flatten plate, anterior margin usually with five teeth.

Pupa.— Form generally stout. Cephalic crest lacking or very small, with rudimenta setae. Mouth parts as in the subfamily, sheaths of maxillary palpi strongly recurv at tips. Pronotal breathing horns subequal in length, short, stout, usually straight, ti but little expanded. Mesonotum transversely wrinkled, in some wood-inhabiting speci (as *T. trivittata*) with about four conspicuous tubercles. Wing sheaths and leg sheat moderate in length. Abdominal armature usually strong, each segment with a posteri row of four to twenty spines; in some species a basal ventral row of spines on posterior ri of segments. Cauda with dorsal armature of four powerful lobes; eighth segment addin as a rule, ten spines, of which six are ventral and lateral in position, and two or four are dorsa dorso-median pair lying between anterior pair of lobes of cauda, as discussed above, an lacking or very reduced in some wood-inhabiting species (*T. trivittata*). Lateral abdomin spiracles lacking or merely vestigial.

Tipula is the largest genus of crane-flies, comprising a vast assembla of species (between six and seven hundred described forms) which a found on all the continental areas of the world but are few in the Austra asian region and apparently lacking on many of the lesser oceanic island The genus is one of extreme interest, and its study will require man years of conscientious application. Subapterous species are not rare i this group, of which many are far northern forms, others are coastal sp cies, while a few live inland and under influences that make it difficult t explain their subapterous condition.

The immature stages of the various species are diverse in their habits, ranging from species that are nearly if not quite aquatic, thru the majority of the known forms which live in generally moist earth or mud along the margins of water bodies, to still others that live in the semi-decayed wood of prostrate tree trunks. Mellor (1919:64) has recorded Tipula larvae as breeding in manure. So far as is known, the larvae are herbivorous, tho they will eat animal food under stress (as described by Patterson [1908] for *Tipula oleracea*, which feeds in considerable numbers on earthworms).

In Europe, a great number of life histories in this genus have been worked out in commendable detail, mainly thru the efforts of Beling, who discusses no fewer than thirty species. His descriptions give a clear idea of the range in structure and habitat to be expected in the genus. The number of lobes surrounding the spiracular disk varies from four (apparently) in *T. selene* and related forms, to as many as eight in *T. subnodicornis*. Practically all of the known species show the normal tipuline number of lobes, six.

A summary of the larval habitats of the Palaearctic species is as follows:

1. Species living in saturated earth along watercourses or in débris at the water's edge, or species that are aquatic — *Tipula fulvipennis* de Geer, *lateralis* Meig., *lunata* Linn., *maxima* Poda, *variicornis* Schum., *variipennis* Meig., *vittata* Meig.
2. Species living in earth, usually in woods, underneath a mold of leaves or coniferous needles — *Tipula caesia* Schum., *dilatata* Schum., *fulvipennis* de Geer, *hortensis* Meig., *hortulana* Meig., *nigra* Linn., *nubeculosa* Meig., *ochracea* Meig., *pabulina* Meig., *paludosa* Meig., *pruinosa* Wied., *scripta* Meig., *selene* Meig., *truncorum* Meig., *unca* Wied., *variipennis* Meig., *vittata* Meig.
3. Species living in earth in gardens, pastures, or meadows, usually beneath turf — *Tipula irrorata* Macq., *luteipennis* Meig., *nigra* Linn., *ochracea* Meig., *oleracea* Linn., *paludosa* Meig., *pruinosa* Wied., *subnodicornis* Zett., *truncorum* Meig., *vernalis* Meig.
4. Species living in or beneath cushions of moss or in earth overgrown with a mossy covering — *Tipula dilatata* Schum., *hortulana* Meig., *marmorata* Meig., *pagana* Meig., *peliostigma* Schum., *pruinosa* Wied., *rufina* Meig., *signata* Staeg., *truncorum* Meig., *unca* Wied.
5. Species living underneath moss on logs — *Tipula irrorata* Macq.
6. Species living in decaying wood — *Tipula flavolineata* Meig., *irrorata* Macq., *truncorum* Meig.

Bouché describes *T. lunata* and *T. ochracea* as living in decaying willow wood, and Sopotzko records *T. flavolineata* as injuring clover; but these records are presumably based on mistaken identifications.

Comparatively few of the eastern American species have been reared, and it is not considered advisable to attempt a key to the larvae or the pupae at this stage of knowledge of the subject. Such a key would

include but a fraction of the possible species and would be of little value. It will require the careful rearing of species for many years before a workable key to the immature stages of the eastern species of the genus can be produced. The characters that will prove of greatest value in the separation of the larvae and the pupae of the species of Tipula are as follows:

Larvae

1. *Anal gills.* (These are rarely lacking, and the number and arrangement of the branches, their form, and their function, are of primary importance.)
2. *Spiracular disk.* Number of lobes surrounding disk and whether they are simple or branched; character and nature of fringe of hairs around disk, if such is present; size, shape, and distance apart of spiracles; markings on inner face of disk and lobes.
3. *Chaetotaxy.* Arrangement, length, and number of setae on segments.
4. *Body form.* Terete, subdepressed, or flattened ventrally only; clothing of pubescence, and pattern formed on dorsum.
5. *Head capsule.* (The head is remarkably uniform thruout the group, a condition to be expected in a group so compact as Tipula.) Shape of mentum and hypopharynx, and number, size, and shape of teeth along their anterior margins; shape of antenna, and other details of head.

Pupae

1. General form, whether terete or depressed.
2. Mouth parts.
3. Pronotal breathing horns, their relative length, size, and form.
4. Armature of mesonotum.
5. Wing sheaths and leg sheaths.
6. Spines on abdominal segments, their size and number; whether lacking or present at base of posterior ring of sternites; arrangement and number of pleural spines.
7. Cauda, shape of genital sheaths, armature of dorsum, and ventral margin of eighth sternite.

Descriptions are given in the following pages of about ten life histories which are entirely new or have been insufficiently considered elsewhere. A few notes on certain other species that have been observed in the past few years may be added here:

Tipula cayuga Alex. A conspicuous yellow larva, living in organic earth beneath leaves, in association with *Bittacomorphella jonesi* and other forms which are discussed elsewhere (page 781). The pupal duration is slightly over seven days.

T. angustipennis Loew. Found living in rather dry earth beneath leaves in shaded woods (Lawrence, Kansas, Mrs. C. P. Alexander).

T. umbrosa Loew. Occurs in garden soil in company with the larvae of *Tipula bicornis* Forbes.

T. fuliginosa Say. Reared from larvae living in débris under the nest of a turkey vulture (Jackson Island, Maryland, May 23, 1913, R. C. Shannon).

T. sayi Alex. and *T. tricolor* Fabr. In saturated mud in marshy or swampy situations.

T. tephrocephala Loew. A large larva, nearly if not quite aquatic in its habits.

The life histories of other Nearctic species are recorded in the summary of literature on page 980. These are as follows: *Tipula arctica* Curt. (Nielsen, Alexander), *T. eluta* Loew (Hart, Malloch), *T. cunctans* Say (Hyslop, Malloch), *T. bicornis* Forbes (Forbes), and *T. ultima* Alex. (Needham, Caudell). *T. arctica*, according to Nielsen (1910:57–59), was found commonly in eastern Greenland. The immature stages were discovered in circular holes from two to three centimeters deep in the ground, especially beneath tufts of *Cassiope tetragona* (L.) D. Don. The pupae were found at the end of June, and empty pupa cases were found as early as the 25th of the same month. According to Nielsen, the larvae require two years to attain their growth.

Tipula (*Trichotipula*) *oropezoides* Johns.

1909 *Tipula oropezoides* Johns. Proc. Boston Soc. Nat. Hist., vol. 34, p. 131–132.

Larvae of *Tipula oropezoides* were first found on March 30, 1917, living beneath saturated moss in Needham's Glen, Ithaca, New York, where they were associated with larvae of *Dicranomyia badia, Penthoptera albitarsis, Tipula collaris*, and other species. Numerous additional larvae were found in the same locality on April 18, 1917. Some of these were placed in rearing and emerged on May 6. The larvae are nocturnal in their habits, being very sluggish and retiring during the day but becoming active after sunset.

The adult flies bear a strong resemblance to species of the genus Oropeza, with which they are sometimes found associated. They may often be swept from rank herbage in cool Canadian woods.

Larva.— Length, 16.5–17 mm.
Diameter, 1.8–2 mm.

Coloration above, a deep velvety brown with mottlings of paler; on basal ring of tergites six median transverse pale spots, posterior ring less regularly marked; pleura and venter pale. (The dark markings on the dorsum are produced by patches of dark-colored hairs, which cover the body densely in places.)

Form subterete. Integument with an abundant pubescence, longest on dorsum. Chaetotaxy as follows: dorsum (Plate XCIII, 516) on posterior ring with six stout setae, three on either side, the middle seta a little closer to the inner seta; ventral segments (Plate XCIII, 517) with four setae, two anterior and two posterior, the latter a little more separated. Spiracular disk (Plate XCIII, 518) surrounded by six approximately subequal lobes, their inner faces heavily lined with dark brown; at tip of each lobe a pale rounded spot, largest on ventral lobes and here with a sensory bristle; lateral mark not reaching spiracles; lateral and dorsal lobes slightly paler medially; above and below each spiracle a transverse brown

line; on disk, between spiracles, two indistinct dusky spots; lobes fringed with rather short, pale hairs which are narrowly interrupted between lobes. Spiracles irregular, roughly triangular. Anal gills four, slender, posterior pair the larger (Plate XCII, 506).

Head capsule as in genus. Labrum and maxilla very densely fringed with long golden-yellow hairs. Mentum (Plate XCIII, 513) with two flattened lateral teeth, the median point elongated; mentum very deeply split behind. Hypopharynx (Plate XCIII, 514) with but three evident teeth, the lateral teeth very broad, flattened. (In some specimens these teeth are all very blunt, so that the anterior margin of the hypopharynx appears merely crenulate.) Antenna with apical disk very flattened. Mandible (Plate XCIII, 515) with a dorsal tooth and a powerful ventral tooth.

Pupa.— Length: male, 12 mm.; female, 12.5–13 mm.
Width, d.-s.: male, 1.6–1.7 mm.; female, 1.8–1.9 mm.
Depth, d.-v.: male, 1.6 mm.; female, 1.7–1.8 mm.

Coloration dark brown; dorsum of thorax and abdomen, and face, more reddish brown. General features as in *Tipula collaris.* Form slender. Pronotal breathing horns long and slender, dark-colored, divergent at tips. Antenna elongate. Wing sheaths ending opposite apex of second abdominal segment. Leg sheaths long, extending to beyond mid-length of fourth abdominal segment. Male cauda with dorsal lobes of genitalia short, blunt; ventral lobes produced caudad into slender, blunt lobes which are transversely wrinkled, separated by a U-shaped notch, at base on outside with a prominent spine. Female ovipositor elongate; dorsal valves narrowed to the blunt tip; ventral lobes stout, a little shorter than dorsal valves, tips strongly divergent; the six dorsal lobes of cauda spinous-tipped, sharply pointed.

Nepionotype.— Ithaca, New York, April 18, 1917. No. 6-1917.
Neanotype.— With type. No. 7-1917.
Paratypes.— Numerous larvae and pupae.

Tipula collaris Say

1823 *Tipula collaris* Say. Journ. Acad. Nat. Sci. Phila., vol. 3, p. 23.

Larvae and pupae of *Tipula collaris,* a common vernal crane-fly, occurred frequently beneath saturated moss (*Amblystegium irriguum* [Wils.] B. & S.) in Needham's Glen, Ithaca, New York, on April 17, 1917. Their associates are noted under the account of *T. oropezoides* (page 1001). In the same moss areas occurred numerous small red-backed salamanders (*Plethedon cinereus*), which probably fed on the insect denizens of the place. Specimens emerged in the writer's breeding jars as late as May 10.

The adults are on the wing during April and May, some persisting into early June in cool northern woods. The life history undoubtedly requires a year for its completion.

Larva.— Length, 21.5–25 mm.
Diameter, 2.5–3.5 mm.

Coloration pale dusky, darker above; dorsum behind with two broken lines which are divergent on each annulus, those of anterior annulus made up of three circular spots; pleura with a conspicuous dark brown stripe; venter almost uniformly pale, with indistinct lines; anterior part of thoracic segments darker. (In life the color is rich reddish brown, and the pleural stripe is not evident.)

Form terete. Body covered with a delicate, pale pubescence, in addition to the usual setae. Chaetotaxy as follows: tergites (Plate XCIV, 521) with a transverse row of six setae on posterior ring before margin, the two innermost solitary, each lateral pair closely approximated; a solitary seta on extreme lateral margins of tergite, at margin of dark pleural stripe, and at about midlength of posterior ring; pleura on basal ring with a single seta, posterior ring with a group of about three or four setae, one larger than the others; sternites with four widely separated setae on posterior ring, the lateral pair a little nearer posterior margin than the median pair. Spiracular disk (Plate XCIV, 522) surrounded by six lobes which are moderately slender; ventral pair a little longer, dorsal pair a little shorter; all the lobes broadly margined with pale brown; ventral lobes having in addition a black capillary line extending from tips backward to beyond midlength of lobes, this line broadest at tip, gradually narrowing, and becoming paler toward base of lobes; below each spiracle, two conspicuous black dots; lobes fringed with numerous rather long hairs. Spiracles large, separated by a distance a little greater than diameter of one. Anal gills six, one pair much shorter than the others, consisting of a basal branch of the anterior gill.

Head capsule rather small, of the usual tipuline type. Mentum (Plate XCIV, 519) very broad, anterior margin almost transverse, seven-toothed, median point the longest. Hypopharynx (Plate XCIV, 520) with five teeth, which are very short and blunt giving anterior margin a deeply crenulated appearance; before hypopharynx a rounded lobe which is densely covered with six short, blunt, chitinized points, this being probably the prementum. Antenna elongate-cylindrical; apex with apical disk very small, button-like. Mandible small, with about one dorsal and two ventral teeth. Maxilla slender, densely hairy; palpus subglobular, with several small, hyaline papillae.

Pupa.— Length, 17–19 mm.
Width, d.-s., 2.8–3.2 mm.
Depth, d.-v., 3–3.3 mm.

Coloration brown; wing sheaths, except in older individuals, pale; pleural region of abdomen light yellow; abdominal incisures often pale.

Head rather small. Cephalic crest low and indistinct, with tiny setae. Labrum broad, apex pointed. Labial lobes oval, contiguous at inner end. Maxillary palpi strongly recurved at tips. Antenna slender, moderately elongated, extending some distance beyond wing root. Pronotal breathing horns equal in length, rather short, the moderately long tips flattened, smooth; two small, approximated setae on either side of median line. Wing sheath (Plate XCIV, 523) extending just beyond end of second abdominal segment; venation distinct. Leg sheaths extending beyond base of fourth abdominal segment; fore tarsi considerably shorter than the others.

Abdominal segments with armature of posterior ring weak, the spines very short and stout, with a few setae; maximum number of spines on the tergites about twenty; lateral anterior angle of posterior ring of tergites with two small spines; pleurites with one basal spine, and

three setiferous spines on posterior ring, arranged transversely; spiracles very rudimentary, opposite base of posterior ring; sternites with spines slightly more numerous and stouter; near base of posterior ring two transverse spines on either side median line, the outermost setiferous. Male cauda on dorsum with six lobes; the four posterior ones stout, with tips spinous or those of ventral pair slightly bifid; the two anterior median lobes shorter and more slender; eighth sternite with four large spines about equally spaced; eighth pleurite with a large, powerful, acutely tipped lobe, and two or three smaller dorso-lateral spines above base of middle pair of dorsal lobes. Female cauda almost the same as male cauda, due to the blunt terebral sheaths of this species.

Nepionotype.— Ithaca, New York, March 30, 1917.
Neanotype.— With type larva.
Paratypes.— Numerous larvae and pupae, March 30 to April 18, 1917.

Tipula nobilis (Loew)

1864 *Pachyrrhina nobilis* Loew. Berl. Ent. Ztschr., vol. 8, p. 62.

Larvae of *Tipula nobilis* were found in wet moss and beneath decaying witch-hazel leaves at Orono, Maine, on June 17, 1913. An adult emerged on July 1. A fully grown pupa found on July 11 attempted to transform but died after two hours without being able to extricate itself from the pupal case.

The adults, which strikingly resemble some species of Nephrotoma, fly somewhat later than does *T. collaris*, but both species may be taken together in early June.

T. nobilis is very similar in all respects to *T. collaris.*

Larva.— Length, 20 mm.
Diameter, 2.9–3 mm.

Coloration, reddish brown.

Spiracular disk as in *T. collaris*, the brown lateral margin to the lobes a little paler. Anal gills as shown in Plate XCII, 507.

Head capsule almost as in *T. collaris.* Mentum with apical point elongate, with three blunt teeth on either side. Hypopharynx with five moderately acute teeth. Antenna with a blunt conical papilla, larger and more conspicuous than in *T collaris.* Mandible with teeth very blunt.

Pupa.— Length of cast pupal skin, about 18.5 mm.

Pupa very similar to that of *T. collaris.*

Nepionotype.— Orono, Maine, June 19, 1913. No. 40-1913.
Neanotype.— With type.

Tipula bella Loew

1863 *Tipula bella* Loew. Berl. Ent. Ztschr., vol. 7, p. 291–292.

Tipula bella is a common species, flying thruout the summer. Larvae nd pupae are not rare in sandy or loamy soil along streams. A larva aken on April 28, 1917, in gravel at Ithaca, New York, where it was ssociated with larvae of Hexatoma, was placed in rearing. It emerged s an adult male on May 15. On May 27, 1913, three fully colored pupae vere found along the sandy banks of Fall Creek, Ithaca, in association vith *Eriocera spinosa*. They emerged as females on May 29 and 30.

Larva.— (The description is from field notes on the larva mentioned above.)

Length, 20–25 mm.

Coloration light grayish brown, with a slight reddish cast most noticeable on venter; orsum with two narrow, almost continuous, dark brown lines, these lines subparallel at nterior part of each segment, then strongly bellied out, and then parallel but finally ivergent.

Spiracular disk surrounded by six rather short lobes; ventral lobes with a linear, rather ale, brown mark, and a few sensory bristles at tips; lateral lobes with ventral margin lined ith brown; dorsal lobes with both margins feebly bordered with brown; two small brown ots below each spiracle. Anal gills six, very long and slender.

Pupa.— Length of cast pupal skin, about 24 mm.

Pupa similar to pupae of other species of genus. Pronotal breathing horns short, ylindrical, narrowed to tips. Spines on abdominal segments rather large, especially on ernites; spines on base of posterior ring of sternites small but evident. Female cauda ith dorsal valves long, pointed; sternal valves shorter. Cauda with the usual six lobes n dorsum, the four posterior stout, divergent, spinous-tipped, the anterior median pair uch smaller; venter of segment 8 with three strong spines on either side, gradually smaller om lateral spine toward innermost spine.

Neanotype.— Ithaca, New York, reared May 25, 1917.

Paratypes.— Pupal skins, type locality, May 5, 1914 (No. 42–1914); August, 1911; May 5, 1917; etc.

'ipula caloptera Loew

1863 *Tipula caloptera* Loew. Berl. Ent. Ztschr., vol. 7, p. 292.

The vigorous larva of *Tipula caloptera* is one of the largest and most triking in the family. The larvae live in rapid- or slow-flowing streams ither in the water among débris and under stones, or in the sand, gravel, r mud in very close proximity to the water. Here they are associated ith the larvae of various species of Eriocera, *Erioptera armata*, Tabanus, therix, and other forms. Oftentimes they are found in deep water in xceedingly lotic situations. A larva placed in rearing on April 19, 1917, merged as an adult female on May 13.

This is evidently the larva taken by Dr. Needham in the Adirondacks and referred by him with some doubt (Needham and Betten, 1901:575-576) to *T. abdominalis*. This dubious reference has created considerable confusion ever since the species was figured on the cover of *Entomological News* under the facetious name "*Quisnam sexcaudatus?*" Malloch (1915-17b:200–201) mentions the same larva under the name *T. abdominalis*. As stated elsewhere, the larva of *abdominalis* is very different.

Larva.— Length, 45–55 mm.
Diameter, 4.8–6.8 mm.

Coloration above, dark brown or brownish green; segments beautifully marked with small white spots, especially anterior segments; a broad, dark brown, median stripe, and a more or less distinct pale lateral stripe (in preserved specimens the pleura is usually dark brown more distinct behind, with numerous pale white dots); sternum dark greenish. (In older specimens the color is very dark and the pattern is more or less obliterated.)

Form stout, terete. Body smooth, segments with indistinct posterior tubercles. Chaetotaxy very weak, a few weak pleural setae on posterior ring, sternal and tergal setae minute Spiracular disk rather small, surrounded by six subequal, moderately narrow, lobes which are fringed with short hairs; margins of disk and lobes somewhat as in *T. bella*, each lobe with a delicate capillary brown line; two brown spots beneath each spiracle. Spiracles small separated by a distance about equal to twice diameter of one. Anal gills six, very long and slender (Plate XCII, 508).

Head capsule as in genus. Mentum broad; anterior margin nearly transverse, with three subacute teeth on either side, median point not conspicuously elongated.

Pupa.— Length of cast skin, about 32–35 mm.

Characters almost as in *T. bella*. Pronotal breathing horns short, cylindrical, tips not expanded. Abdominal spines prominent, projecting, few in number, on intermediate tergites 9 or 10; pleurites with a single strong spine on each ring; sternites with a posterior row of seven or eight strong spines; on segments 5 to 7 two strong spines at base of posterior ring, those of seventh segment the largest. Cauda almost as in *T. bella*.

Nepionotype.— Ithaca, New York, April 26, 1917. No. 16-1917.
Neanotype.— Cast pupal skin, reared May 13, 1917.
Paratypes.— Larvae and cast pupal skins from type locality.

Tipula dejecta Walk.

1856 *Tipula dejecta* Walk. Ins. Saunders, vol. 1, Dipt., p. 442.
1901 *Tipula fumosa* Doane. Journ. N. Y. Ent. Soc., vol. 9, p. 99.

Tipula dejecta is a characteristic vernal species flying in April and May The flies are notable inhabitants of swamps, especially alder swamps.

On April 20, 1917, the writer found larvae of this fly in Larch Meadows near Ithaca, New York, in association with larvae of *Rhamphidia mainensis*, *Pseudolimnophila luteipennis*, and other swamp inhabitants. Th

conditions are discussed more fully under the account of Rhamphidia (page 831). The larvae are reddish brown in color, and rather sluggish. One of the larvae found on April 20 pupated on the 22d and emerged as an adult female on the 30th, a pupal duration of eight days. An additional pupa was taken, associated with larva of *Pseudolimnophila luteipennis*, *P. inornata*, *Tricyphona inconstans*, and other species.

Larva.— Length, 20 mm.
Diameter, 1.8 mm.

Coloration brown; dorsum marked with light and dark brown; a narrow, indistinct, dark brown, median line, with a broader zigzag brown line on either side; ventral surface a little paler.

Body covered with a short, dark pubescence at sides of segments, at margins longer and more conspicuous. Chaetotaxy as follows: tergites with six strong setae in transverse alinement, the outermost in pairs; two strong setae on each pleural annulus; posterior ring of sternites with eight strong setae, arranged in four pairs. Spiracular disk (Plate XCV, 526) pale, surrounded by six approximately equal lobes which are heavily marked with brown; dorsal and lateral pairs pointed, ventral pair blunt; ventral lobes with apical half shiny black, on ventral inner margin continued dorsad, almost contiguous on midline; inner face of dorsal and lateral lobes suffused with dark brown, proximal margin of dorsal lobe produced inward so that the marks are almost contiguous on median line; beneath each spiracle a transversely rectangular, dark brown mark. Anal gills with four anterior lobes which are long and slender, and a pair of rudimentary blunt posterior gills (Plate XCII, 509).

Head capsule and mouth parts as in genus. Mentum (Plate XCV, 524) seven-toothed, apical point the longest. Hypopharynx (Plate XCV, 525) bluntly five-toothed.

Pupa.— Length, 15.3 mm.
Width, d.-s., 2.3–2.4 mm.
Depth, d.-v., 2.1–2.2 mm.

Coloration dark brown; abdominal incisures paler.

Form relatively stout. General features as in genus. Cephalic crest consisting of two blunt lobes with microscopic setae. Maxillary palpi strongly curved at tip, but not entirely recurved. Pronotal breathing horns short, tips a little enlarged.

Abdominal tergites with spines weak, on median area of each row weak or lacking; on intermediate segments about fifteen spines; pleurites with only a single weak spine on basal ring; on posterior ring a rudimentary anterior spine and a somewhat larger posterior spine; sternites similarly armed to tergites, but spines fewer in number and larger, on segment 5 about twelve in number; on base of posterior ring a large spine on either side median line and a small setiferous tubercle laterad of each. Female cauda with tergal valves of ovipositor long and straight, sternal valves a little shorter; cauda with the usual six dorsal lobes, these terminating in slender spines; at end of eighth sternite six large spines; dorsal spines reduced to a single small pair, one near each lateral margin.

Nepionotype.— Larch Meadows, Ithaca, New York, April 20, 1917.
Neanotype.— With type.
Paratypes.— Two pupae with type pupa.

Tipula usitata Doane

1901 *Tipula usitata* Doane. Journ. N. Y. Ent. Soc., vol. 9, p. 124.

A large number of fully grown larvae of an unknown species of Tipula were found beneath the bark of a fallen tree at Stanford University, California, on March 22, 1915, by Harold Morrison. They were sent to the writer at Ithaca, New York, and emerged as adults on April 15. The immature stages are very distinct, closest perhaps to *T. trivittata*, which also lives beneath the bark of decaying trees. Nothing is known of the habits of the adult flies.

Larva.— Length, 25–27 mm.
Diameter, 3–3.2 mm.

Coloration pale greenish yellow, darker above.

Form terete. Body with a very sparse pubescence. Chaetotaxy as follows: tergites (Plate XCV, 527) with a posterior row of eight setae, the middle pair of each side very closely approximated; a seta near lateral margin at base of posterior ring, on a level with pleural seta; pleurites, one seta on each ring; sternites with eight setae in closely approximated pairs on posterior ring. Spiracular disk (Plate XCV, 528) surrounded by six lobes; dorsal and lateral pairs slender, tips of former acute; ventral lobes blunt; ventral lobes with tips blackened, continued down proximal margin of lobes as a paler brown line; lateral lobes with inner face narrowly blackened, this mark not reaching spiracles; dorsal lobes with entire inner face bulging, intensely black, the marks contiguous at their basal inner angle; an indistinct brown spot underneath each spiracle, in some specimens this mark continuous with that of ventral lobes; lobes not fringed with hairs. Spiracles large, separated by a distance about equal to, or a little greater than, diameter of one. Anal gills short and blunt, strongly protuberant, surrounding anus as four fleshy lobes (Plate XCII, 510).

Head capsule as in genus. Mentum broad, with seven to nine teeth, in the latter case the outermost pair very small. Hypopharynx with three or five very blunt teeth. Antenna much shorter and stouter than in most species of Tipula, the length only a little greater than twice the diameter, at apex with a blunt conical papilla and a few small, cylindrical sense pegs. Mandible powerful, with two or three flattened teeth on ventral cutting edge.

Pupa.— Length, 15–16.8 mm.
Width, d.-s., 2 mm.
Depth, d.-v., 2.3–2.4 mm.

Coloration pale brown; posterior margin of abdominal rings pale; lateral margin of abdomen conspicuously pale yellowish white.

Form slender. Pronotal breathing horns narrow, a little expanded at tips. Leg sheaths ending on a level.

Abdominal spines very strong, but few in number; tergites with four to six spines; pleurites with a single weak spine on each ring; sternal spines very strong, five or six in number, those on segment 7 subequal in size to those on segment 8; no sternal spines on base of posterior ring. Male cauda with posterior dorsal lobe very strong, pale, tips acute; lateral lobes greatly

reduced in size, the median pair represented only by two blunt brown tubercles; eighth segment with the usual six strong ventral and lateral lobes. Female ovipositor with valves small; sternal valves short and broad, much shorter than tergal valves.

Nepionotype.— Stanford University, California, April 15, 1915.
Neanotype.— With type, bred April 15, 1915.
Paratypes.— Numerous larvae and pupae with type.

Tipula trivittata Say

1823 *Tipula trivittata* Say. Journ. Acad. Nat. Sci. Phila., vol. 3, p. 26.

The larvae and the pupae of *Tipula trivittata* live beneath the bark of much-decayed prostrate trunks or under the layers of moss that often cover fallen trees. Abundant larvae were found on March 22, 1913, and were placed in rearing, adults emerging on April 26. On April 16, 1914, larvae of two distinct sizes —some very small and some nearly fully grown — occurred in abundance beneath moss (*Entodon seductrix* [Hedw.] C. Muell., *Brachythecium acuminatum* [Hedw.] Kindb., *Hypnum Haldanianum* Grev., and *Mnium sylvaticum* Lindb.) on prostrate decaying elms, sycamores, and other trees, at Renwick Park, Ithaca, New York.

The adult flies are among the commonest of the eastern species of Tipula, and fly during a large part of the season.

Larva.— Length, 24–25 mm.
Diameter, 2.7–3 mm.

Coloration pale brownish yellow, a little paler beneath.

Form moderately elongated, terete. Pubescence very short or practically lacking. Setae on anterior segments strong, on posterior segments shorter. Chaetotaxy as follows: tergites with a posterior row of six setae, the two middle punctures each with a single seta, the two lateral punctures each with two setae; pleurites with a single seta on each ring; sternites with two rows of setae, the anterior row consisting of two closely approximated groups of two setae each, the posterior row consisting of a single large seta, laterad of which is a minute bristle. Spiracular disk (Plate XCV, 529) surrounded by six lobes; lateral pair long and slender; dorsal pair a little shorter, slender; ventral lobes blunt; ventral lobes with a jet-black mark on inner face; lateral lobes with dark markings represented only by a very small linear dash; dorsal lobes with a small black area. Spiracles large, separated by a distance a little less than diameter of one. Anal gills indistinctly lobed, four in number, two on either side, very blunt and protuberant.

Head capsule as in genus, the mouth parts almost as in *T. usitata.* Mentum broad, with seven teeth. Hypopharynx with five teeth, the three middle ones the longest, subequal in size. Antenna shorter and stouter than is usual in the genus.

Pupa.— Length, 19–20 mm.
Width, d.-s., 2.5–2.6 mm.
Depth, d.-v., 2.8–3 mm.

Coloration dark brown; abdomen yellow, with a broad sublateral brown stripe on both sternites and tergites; abdominal segments beyond posterior row of spines brighter, more yellowish.

Characters of head as in genus. Cephalic crest very small. Labrum broad. Pronotal breathing horns short, slightly curved. Mesonotal prescutum with fine transverse wrinkles; two blunt lateral tubercles, and behind these, on either side of median line, two smaller flattened ledges which are often bifid at their tips. (Similar ledges, but much less prominent, occur in *T. usitata.*)

Abdominal tergites with subapical armature weak, spines varying in number from six to eight, those of posterior segments larger; pleural spines long and slender, one on each ring; sternal spines powerful, four to six in number, no spines on base of posterior ring. Female cauda with sternal valves long and slender, but little shorter than tergal valves; dorsal lobes of cauda four in number, posterior pair very powerful, lateral pair small, anterior median pair lacking.

Nepionotype.— Ithaca, New York, March 22, 1913.
Neanotype.— With type.
Paratypes.— Numerous larvae and pupae with types, April 26, 1917; March 22, 1913; etc.

Tipula ignobilis Loew

1863 *Tipula ignobilis* Loew. Berl. Ent. Ztschr., vol. 7, p. 280.

The adult flies of *Tipula ignobilis* are not common in collections, due in part to their retiring habits. The larvae, however, are common in their preferred habitat, saturated moss cushions.

At Orono, Maine, numerous larvae were taken in wet moss on June 17, 1913, associated with other larvae, such as those of Rhaphidolabina, Tricyphona, Pedicia, and *Tipula nobilis*. At Ithaca, New York, on April 23, 1917, four very small larvae were found in wet cushions of moss (Amblystegium). They grew very rapidly, emerging as adults on May 21. On May 22 this moss was carefully examined and about thirty fully grown to rather immature larvae of this species were taken. They were associated with equally numerous larvae of *Dicranomyia stulta* O. S. At Needham's Glen, the species occurred in the same moss that earlier in the season harbored *Tipula collaris* and *T. oropezoides*. On June 1[illegible] two teneral adults of *T. ignobilis* were captured, in company with *Dicranomyia stulta*, *Geranomyia canadensis*, *Dactylolabis montana*, and other species. The species is very common at the Indian Ladder, Helderberg Mountains, New York.

Larva.— Length, 16.5–18 mm.
Diameter, 2.5–2.6 mm.

Coloration grayish brown, paler gray beneath; thoracic segments conspicuously reddish rown.

Body terete. Dorsum covered with a short, dark pubescence, which gives upper surface ts dark color. Chaetotaxy as follows: tergites (Plate XCVI, 530) with a posterior transerse row of two setae near base of posterior ring; sternites (Plate XCVI, 531) with about ight setae, anterior median row consisting of two large setae, each with a tiny seta roximad of it, the posterior pair of large setae more widely separated, laterad of each of these wo closely approximated smaller setae. Spiracular disk (Plate XCVI, 532) surrounded y six moderately long lobes fringed with rather short, pale hairs; tips of ventral lobes with pale circular area provided with a sensory seta; inner face of spiracular disk with the narkings pale, ventral lobes with an indistinct capillary brown line; two brown spots beneath ach spiracle. Spiracles large. Anal gills eight, consisting of a transverse row of four hort, slender, two-branched lobes (Plate XCII, 511).

Mentum of head capsule with median point prominent, the three lateral teeth of either ide small, moderately acute. Mandible with about four teeth, in addition to the large asal prosthecal tooth.

Pupa.— Length: male, 12 mm.; female, 14–15 mm.
Width, d.-s.: male, 1.7–1.8 mm.; female, 1.8–2 mm.
Depth, d.-v.: male, 1.9–2 mm.; female, 2.1–2.2 mm.

Head and mouth parts as in genus. Pronotal breathing horns rather long and slender, ps a little expanded. Leg sheaths rather short, just exceeding third abdominal segment; ind legs a little the longest, the other tarsi ending about on a level.

Abdominal tergites with armature weak, spines small; pleurites and sternites with spines otably larger and more powerful; sternites with subterminal row consisting of twelve to fteen spines, those of the sixth and seventh segments larger; no spines at base of posterior ng; pleural spines setiferous, very weak, one on basal ring, two on posterior ring. Male uda with ventral lobes widely separated, terminating in slender, curved spines directed udad; dorsal lobes slender, approximated on dorso-median line. Female cauda (Plate CVI, 533) with tergal valves a little longer than sternal valves, the latter at their tips rminating in slender points directed ventrad and laterad; dorsum of cauda with the usual x lobes, posterior pair the largest, terminating in two distinct points; eighth segment on leural and sternal region with six very powerful, curved spines.

Nepionotype.— Ithaca, New York, June 3, 1917.
Neanotype.— With larva, June 3, 1917.
Paratypes.— Numerous larvae and pupae, June 1 to 12, 1917.

ipula abdominalis (Say)

1823 *Ctenophora abdominalis* Say. Journ. Acad. Nat. Sci. Phila., vol. 3, p. 18.

Tipula abdominalis is the largest eastern species of the genus, altho ome specimens of *T. caloptera* are nearly as large. The adult flies are n the wing in late August and September, and even, in fewer numbers, June and July.

The large, fleshy larvae occur beneath or among drift at or near the margins of streams. They are usually abundant under saturated decaying leaves or under tussocks of grass at the edge of the water. They are entirely herbivorous, feeding on diatoms, decaying plant tissues and other vegetable matter. The larvae are readily distinguished from all other species of the genus by the small spiracles and the bifid or split lobes surrounding the spiracular disk. Pupation takes place in the mud or earth at the water's edge. Malloch's *Tipula* sp. 2 (1915–17b: 200-201) seems to refer to *T. abdominalis*, but the mouth parts of his specimens do not seem to be normal.

Larva.— Length, 55–65 mm.
Diameter, 7.5–10 mm.

Coloration pale grayish brown; anterior end darker.

Form stout, terete, thin-skinned. Posterior ring of abdominal segment, both above an[d] below, with a naked transverse welt, which bears the setae; this welt very protuberant a[t] its lateral ends, almost like a pair of prolegs. Skin naked, except for a microscopic dottin[g] and the rather short, delicate setae. Chaetotaxy as follows: tergites, on welt at about mi[d] length, a transverse row of eight setae, the middle pair of each half closely approximate[d]; pleurites with a single seta opposite basal ring, and two opposite posterior ring, arrange[d] one behind the other; sternites with four pairs of setae on welts, anterior middle pair close[r] together than posterior lateral pair. Spiracular disk (Plate XCVII, 537) moderately larg[e], flattened, truncated, surrounded by six deeply bifid and irregular lobes; ventral lobes elo[n]gate, with a blunt basal branch bearing two setae; posterior branch longer, indistinctl[y] bifid at tip and with a few setae and several hairs; lateral lobes deeply bifid, the ventr[al] one armed with lateral setae; dorsal lobes small, simple; inner faces of dorsal and later[al] lobes with a narrow dark brown stripe, ventral lobes with two narrow, usually indistin[ct] lines, these markings broadest and darkest on dorsal lobes. Spiracles very small, circula[r], separated by a distance about equal to four times diameter of one. Anal gills six, long a[nd] slender, the middle one on either side a little shorter than the others. Pleural region [of] penultimate segment of body with a blunt setiferous tubercle.

Head capsule and mouth parts about as in genus. Mentum (Plate XCVII, 536) broad[,] transverse, anterior margin with seven to nine teeth, in the latter case the outermost tee[th] very indistinctly separated from the sublateral teeth. Hypopharynx broad, anterior marg[in] with teeth very indistinct.

Pupa.— Length of cast pupal skin, about 35 mm.

Pronotal breathing horns short, straight, cylindrical; apex short, and but little if at [all] expanded. Details of mouth parts as in other species of genus. Wing sheaths endi[ng] before apex of second abdominal segment. Leg sheaths extending to about opposite e[nd] of third abdominal segment; fore tarsi the shortest, hind tarsi the longest, ends of tar[sal] sheath thus forming a broad, inverted U-shaped notch.

Abdominal armature generally weak. Tergites (Plate XCVII, 538) with subterminal r[ow] broken, consisting of an anterior median pair of large spines, laterad of which are two

three smaller spines; close to ends of row a bifid setiferous spine; pleurites with spines long, slender, directed strongly caudad, tips narrowly bifid, bearing a seta in notch; basal spine the largest; posterior spines two in number, anterior dorsal one the smaller; sternites (Plate XCVII, 539) with posterior row unbroken, of comparatively few spines, there being about eleven excluding the two larger spines at ends of row; the innermost of the large lateral spines conspicuously bifid, bearing a stout seta in its notch; base of posterior ring on either side of median line with a powerful conical spine which is acutely tipped. Female cauda as in genus, sternal valves conspicuously shorter than the long tergal valves; the six dorsal lobes powerful, chitinized, more or less bifid at tips; dorsal lateral lobes at end of eighth segment split before tips.

Nepionotype.— Cascadilla Creek, Ithaca, New York, May 31, 1913.
Neanotype.— Cast pupal skin, reared at Ithaca, September, 1911.
Paratypes.— Abundant larvae from type locality.

Tipula taughannock Alex.

1915 *Tipula taughannock* Alex. Proc. Acad. Nat. Sci. Phila., p. 476–479.

Tipula taughannock is of exceptional interest in the striking color dimorphism that it shows, the females being black and yellow, the males light yellowish. The following account of the habits of the adult flies is taken from the writer's field notes:

June 12, 1915. Deciduous forest association of the southern Helderberg Mountains, near the village of New Salem, Albany County, New York. This association is an open deciduous forest, with an undergrowth of Cystopteris, Geranium, Caulophyllum, and Impatiens. It is a very open woods, having an eastern exposure and with the talus slopes so old that an extensive vegetation has sprung up. The great boulders scattered about thru the woods have come from the high Silurian and Devonian cliffs above. The woods are of such a nature that much sunlight penetrates to the ground beneath. The forest cover shows a striking lack of coniferous species, but the following deciduous species are common: butternut, hop hornbeam, hard maple, basswood, white ash. The shrubbery consists of mountain maple, bladdernut, and a few dogwoods. The dominant herbage consists of jack-in-the-pulpit, wild ginger, bloodroot, bishop's-cap, false bishop's-cap, blue cohosh, white baneberry, herb robert, touch-me-not, waterleaf, bedstraw, and other characteristic flowering plants in fewer numbers, as well as several ferns, such as the bulbous bladder fern, maidenhair, and, on the rocks, the walking fern. The crane-fly under consideration is very common in these woods. The proportion of males to females is about one hundred to one, but this is due, in large part at least, to the very secretive habits of the latter. The males are untiring, almost always flying along, silently and relentlessly, in quest of their mates. They pass in and out among the dense herbage, usually close to the ground, occasionally fluttering up a tree trunk or over a mossy boulder which is covered with various bryophytes and walking ferns. They are so intent upon their quest that they are readily scooped up by hand. If this is attempted and fails, however, they become instantly alarmed and fly away with great speed, their flight at this time having a strong undulating motion. In a position of rest, the male almost always hangs on the under surface of a leaf, with the body directed straight toward the ground. Several specimens of this species, as well as of *Tipula trivittata* Say and *T. senega* Alex., were found dead in spider's webs. These small webs, made by species of Theridiidae and Linyphiidae, are very common on and between the leaves of herbaceous plants and are presumably intended for smaller game. The large Tipulas are probably taken in by accident.

The females are more active when in flight than are their mates and are capable of moving very rapidly. Their flight is a rapid, fluttering progression along the ground. Copulation takes place on either the upper or the lower surface of leaves, usually near the ground. Sometimes copulation is end to end, with the heads directed away from each other; at other times it is face to face, the bodies being arcuated into a convex loop.

The larva almost certainly lives among or beneath the decaying leaves and débris which cover the talus slope.

Tipula macrolabis Loew

1864 *Tipula macrolabis* Loew. Berl. Ent. Ztschr., vol. 8, p. 58.

Tipula macrolabis is distinctly northern in its distribution. It is a characteristic fly of northern deciduous woods in June. The following notes were made near the village of Indian Castle, Herkimer County, New York, on June 13, 1915:

A small woodland stream with a forest cover of trees such as hemlock, beech, slipper elm, and basswood, and a ground cover of false solomon's seal, wood nettle, wild ginger herb robert, touch-me-not, waterleaf, sarsaparilla, and the two abundant ferns maidenhai and the bulbous bladder fern. The males of *T. macrolabis* were in search of the females and fluttered up the tree trunks often to a height of ten or fifteen feet, flying close to th ground, around brush heaps, hovering about the leafy ends of branches, and performin similar actions in their untiring quest for their mates. They occurred in company wit males of *T. fuliginosa* and *T. valida*, which were similarly engaged in searching for the females

Tipuline No. 1 (possibly *Tipula iroquois* Alex.)

1863 *Tipula cincta* Loew. Berl. Ent. Ztschr., vol. 7, p. 288–289, not *T. cincta* Gmel. Syst. Nat., ed. 13, vol. 1, p. 2820 (1792).
1915 *Tipula iroquois* Alex. Insec. Inscit. Menst., vol. 3, p. 128.

The larva discussed below has never been reared and is mentione here principally because of its interesting habitat. It is referred t *Tipula iroquois* with considerable doubt.

The larva lives among dense mats of an aquatic moss, a Hypnur (Rhynchostegium) of the *dilatatum* group, in the most rapid-flowin streams. At Coy Glen, Ithaca, New York, these larvae are especiall frequent, often living at the brink of falls or rapids in the most rushin waters. A study of the structure of the larva reveals numerous sma but prominent tubercles, which doubtless assist the insect in clinging t the moss stems. The gills are large, but no better developed than i many aquatic species of the genus that live in much less lotic condition The green color and the transverse rows of tubercles on the body give th larva a strong resemblance to its mossy habitat. The larvae are ver sluggish and crawl but slowly, often appearing quite dead for long period of time.

Associated with these larvae in Coy Glen, the following characteristic forms of insect life occur:

Plecoptera: a small species of Perlidae.
Ephemerida: Ephemeridae, such as Baetis, *Iron fragilis*, Ephemerella, and others.
Trichoptera: Ryacophilidae, Hydroptilidae, and other forms.
Neuroptera: Chauliodes larvae.
Diptera: Chironomidae, a few; Psychodidae, *Psychoda albitarsis* Banks; Stratiomyiidae; Anthomyiidae, *Limnophora torreyae* Joh.; and other groups.
Coleoptera: Parnidae, larvae of *Psephenus lecontei* (Lec.), and adult beetles of a species of Elmis in large numbers.

Up to the present time it has been found impossible to rear this larva to the adult condition, chiefly because of the constant need of well-aërated water and the difficulty of supplying it. By placing the larvae in the folds of moistened cheesecloth, it was possible on one occasion to carry the species to the pupal state, but no further. It will be of interest to ascertain the identity of this conspicuous larva.

Larva.— Length, 24–25 mm.
Diameter, 2.6–3 mm.

Coloration above, dark green with a brown pattern; beneath, light green with indistinct transverse brown lines; on dorsum a pale longitudinal mark on sides of posterior ring, crossing sutures between segments onto extreme base of anterior ring of following segment, the dark area of each segment thus appearing cruciform, this cross-shaped mark spotted and marbled with darker in transverse rows; base of gills and center of spiracular disk light green in living, healthy larvae.

Form moderately terete, each segment with transverse rows of small, prominent tubercles, some of which are provided with setae. On dorsum of posterior ring a subterminal row of six tubercles, the middle one on each side with two setae, the remaining four tubercles unisetose; two rows of smaller naked tubercles at base and middle of posterior annulus; basal annulus with four transverse rows of small naked tubercles; pleurites with three tubercles, a small seta on basal ring ventrad of basal tubercle, and two setae on posterior ring ventrad and cephalad of posterior tubercle; sternites on posterior ring with six setae, four on anterior row, the two middle ones very tiny. Spiracular disk almost as in *T. collaris*, *T. ignobilis*, and similar species, surrounded by six lobes fringed with moderately long hairs; inner face of lobes somewhat pale; ventral lobes with a narrow, capillary, dark brown line, extending from tip toward base; lobes narrowly and more or less indistinctly margined with brown; two brown spots at base of each ventral lobe, underneath each spiracle; dorsal and lateral lobes jutting backward at tips into fleshy conical points. Spiracles circular, moderately large, separated by a distance about equal to one and one-half diameter of one. Anal gills with eight branches, rather short and stout, with two lateral divergent branches on either side and an inner pair with one ventral and one posterior branch (Plate XCII, 512).

Head capsule and mouth parts of almost normal tipuline appearance. Mentum with outer plate forming the unusually long apical point, inner plate adding three teeth on either side, margins bulging. Antenna with apical papillae somewhat flattened, surrounded by three sense pegs.

(Described from abundant specimens, Coy Glen, Ithaca, New York, April 23, 1914.)

Tipuline No. 2

The larva discussed below is known only from a single, apparently fully grown, specimen. The writer has no clue as to which species it represents, altho from the larval structure it is obviously allied to *Tipula selene* Meig. of Europe.

Larva.— Length, 23 mm.
Diameter, 3 mm.

Coloration, a rather uniform pale yellowish or reddish brown.

Body covered with a rather sparse, long pubescence, setae unusually long and powerful. Chaetotaxy as follows: tergites (Plate XCVI, 534) with two strong lateral setae near posterior margin and an additional one at extreme lateral margin of ring; pleural setae, one on basal ring, two, one behind the other, on posterior ring; sternites with a transverse pair of powerful setae near extreme lateral margin, and two anterior pairs of much smaller setae. Spiracular disk (Plate XCVI, 535) with four elongated, cylindrical, chitinized horns which are narrowed to the acute, blackened, slightly curved tips; longer dorsal pair rather closely approximated, lying almost parallel, with tips a little curved dorsad; shorter and more slender lateral horns directed ventrad at tips, at base on inner face with a powerful seta, the large black spiracles lying above base of lateral horns; ventral lobes, if present, very blunt and indistinct. Anal gills not protruded in the only specimen available.

Head capsule and mouth parts rather normal but showing the following points of difference from the usual Tipula type: Mentum almost completely split, apical point long and narrow; the three lateral teeth on either side blunt, lateral pair tending to be reduced.

Hypopharynx with five blunt teeth. Antenna short, stout, length only about twice diameter, at tip with a subglobular, feebly chitinized papilla.

(Described from a single larva found beneath a stone in a field near Taughannock Falls, Tompkins County, New York, May 1, 1912.)

Genus **Nephrotoma** Meigen (Gr. *kidney* + *I cut*)

1800 *Pales* Meig. Nouv. Class. Mouch., p. 14 (*nomen nudum*).
1803 *Nephrotoma* Meig. Illiger's Mag., p. 262.
1834 *Pachyrrhina* Macq. Hist. Nat. Ins., Dipt., vol. 1, p. 88.

The large genus Nephrotoma, including some one hundred and fifty described species, is very close to Tipula in all respects. The writer cannot attempt to separate the immature stages of the genus from those of Tipula, on the scanty material that has been available for study.

In Europe, Beling and others have described the life histories of about eight of the commoner species. The following species live in earth, beneath a covering of leaf mold: *analis* (Schum.), *cornicina* (Linn.), *lineata* (Scop.), *maculata* (Meig.), *lunulicornis* (Schum.), *pratensis* (Linn.). The following have been described as living in decaying wood, some of the records apparently being in error: *cornicina* (Linn.), *crocata* (Linn.), *lineata* (Scop.), *quadrifaria* (Meig.). Some of the species are injurious to young seedlings, especially those of coniferous plants.

In North America the commonest species, *N. ferruginea* (Fabr.), has been discussed several times in its economic relations to agriculture. Hart (1898 [1895]:218–219) gives an excellent description of the immature stages, while Malloch (1915–17 b:206) gives supplementary notes and figures of the same species. The immature stages live in sand or earth. *N. virescens* (Loew) was bred from a larva found in moss on Plummers Island, Maryland, on April 5, 1913, by R. C. Shannon. *N. eucera* (Loew) and *N. polymera* (Loew) have been reared from larvae taken under leaf mold in woods by Mabel M. Alexander.

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EXPLANATION OF ABBREVIATIONS USED ON PLATES

A=antenna	Pl=pleuron
C=cardo	PM=prementum
Lb=labium, or labial lobes	S=stipes
M=mentum	SM=submentum
Md=mandible	Sp=spiracle
Mx=maxilla	St=sternite
P=palpus, or palpal sheath	T=tergite

Memoir 34, *An Economic Study of Farm Layout*, the fourth preceding number in this series of publications, was mailed on January 31, 1921.

Memoir 35, *Some Effects of Potassium Salts on Soils*, the third preceding number in this series of publications, was mailed on January 29, 1921.

Memoir 36, *Resistance of the Roots of Some Fruit Species to Low Temperature*, the second preceding number in this series of publications, was mailed on January 19, 1921.

Memoir 37, *A Modified Babcock Method for Determining Fat in Butter*, the next preceding number in this series of publications, was mailed on December 10, 1920.

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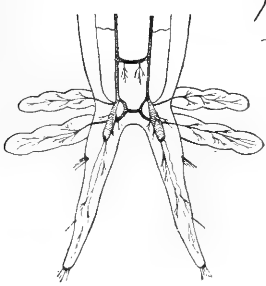

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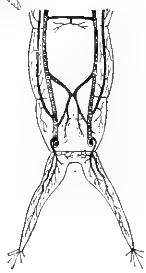

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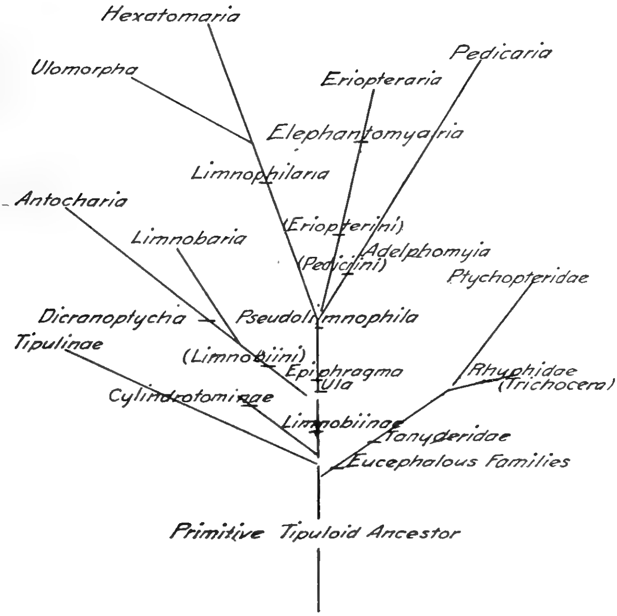
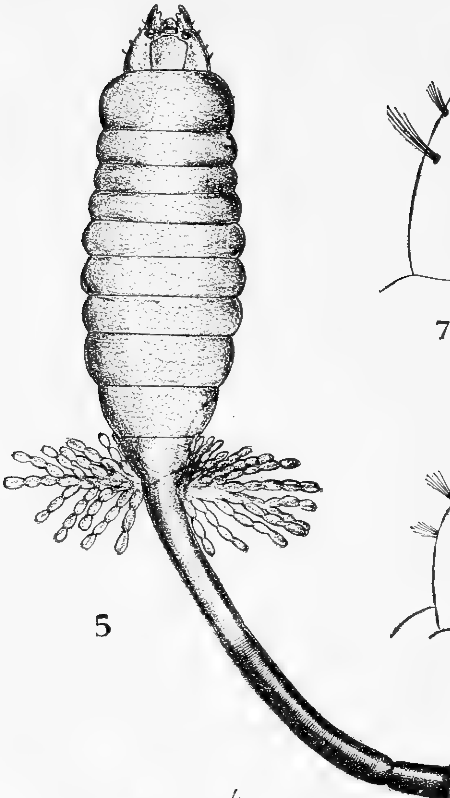


4

1, *Eriocera spinosa* emerging from pupal hull.

2–3, Spiracular disk and tracheation of larvae: 2, *Antocha saxicola* (apneustic); 3, *Dicranota bimaculata* (metapneustic), after Miall

4, Phylogenetic tree



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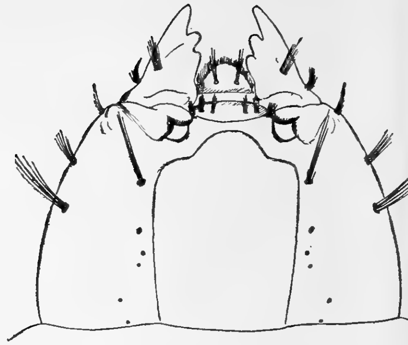

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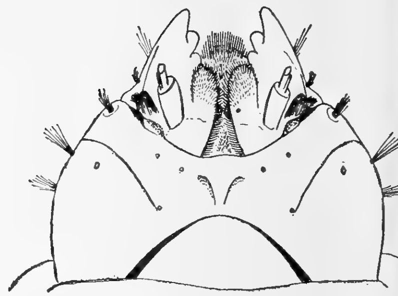

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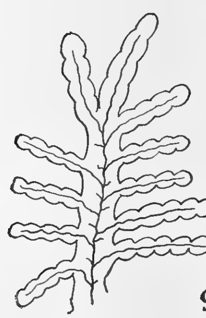
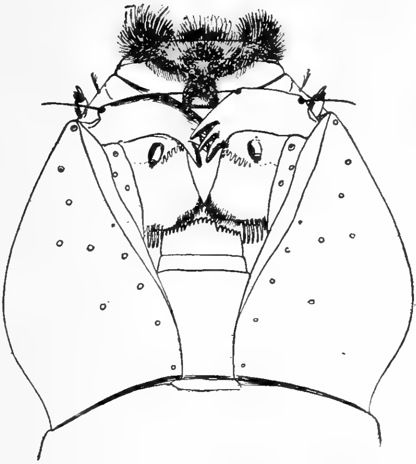


9

PROTOPLASA FITCHII, SUPPOSITION

5, Dorsal aspect; 6, spiracular disk; 7, head, dorsal aspect; 8, head, ventral asp
anal gill

0



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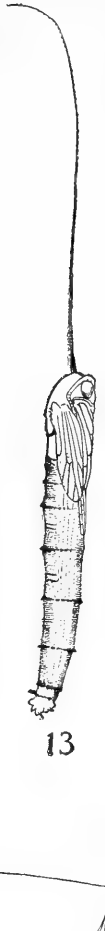

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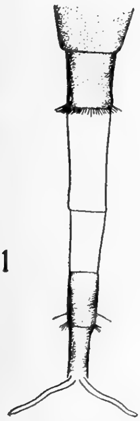

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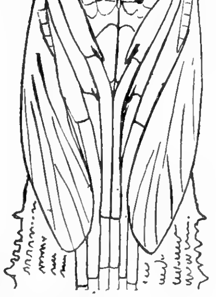

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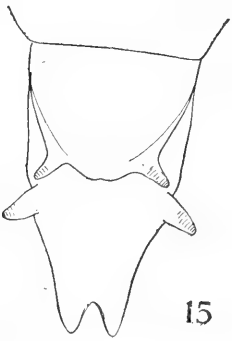
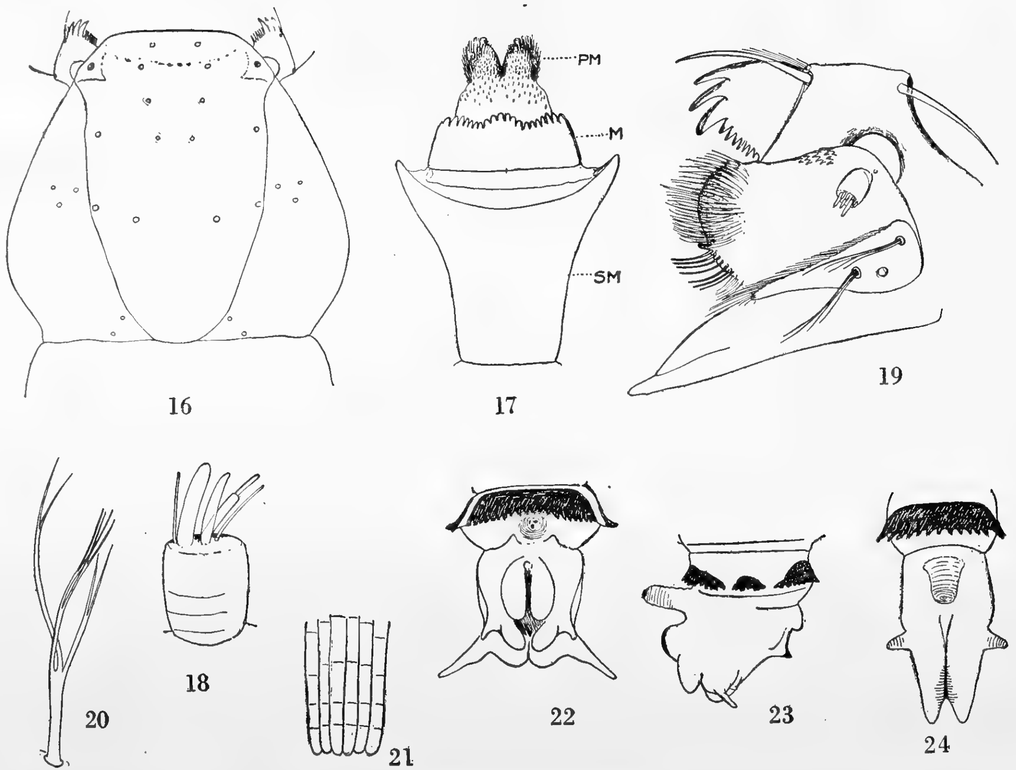


15

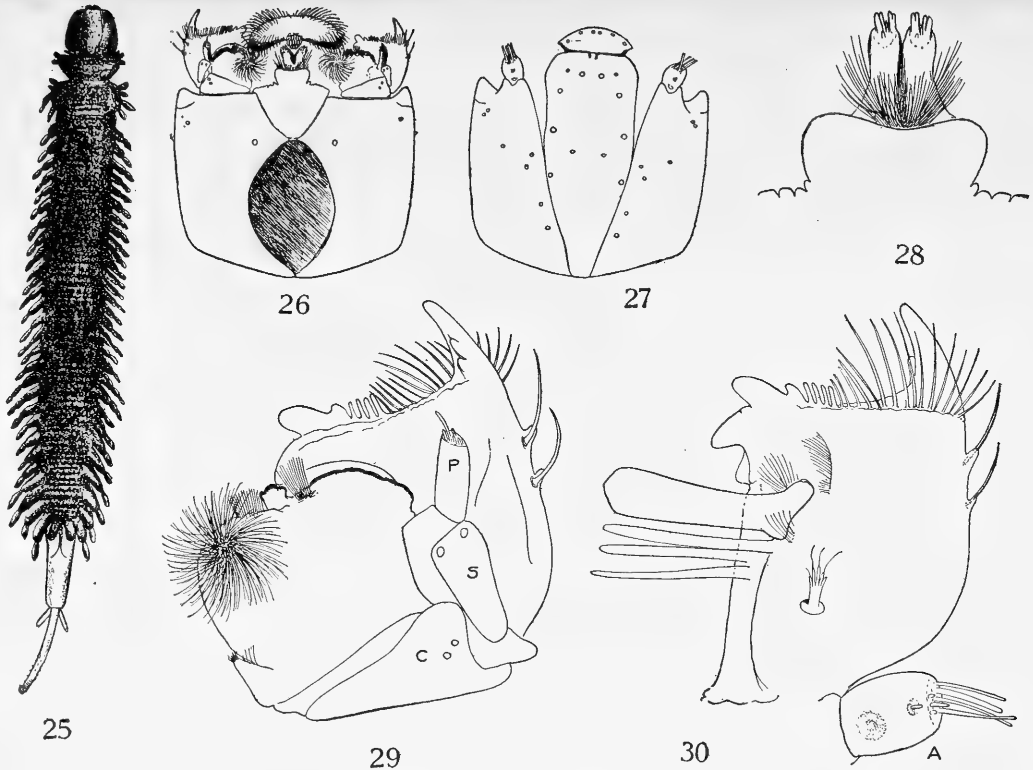
PTYCHOPTERA RUFOCINCTA

Larva: 10, dorsal aspect; 11, breathing tube extended; 12, head, ventral aspect
Pupa: 13, lateral aspect; 14, ventral aspect; 15, female cauda, ventral aspect



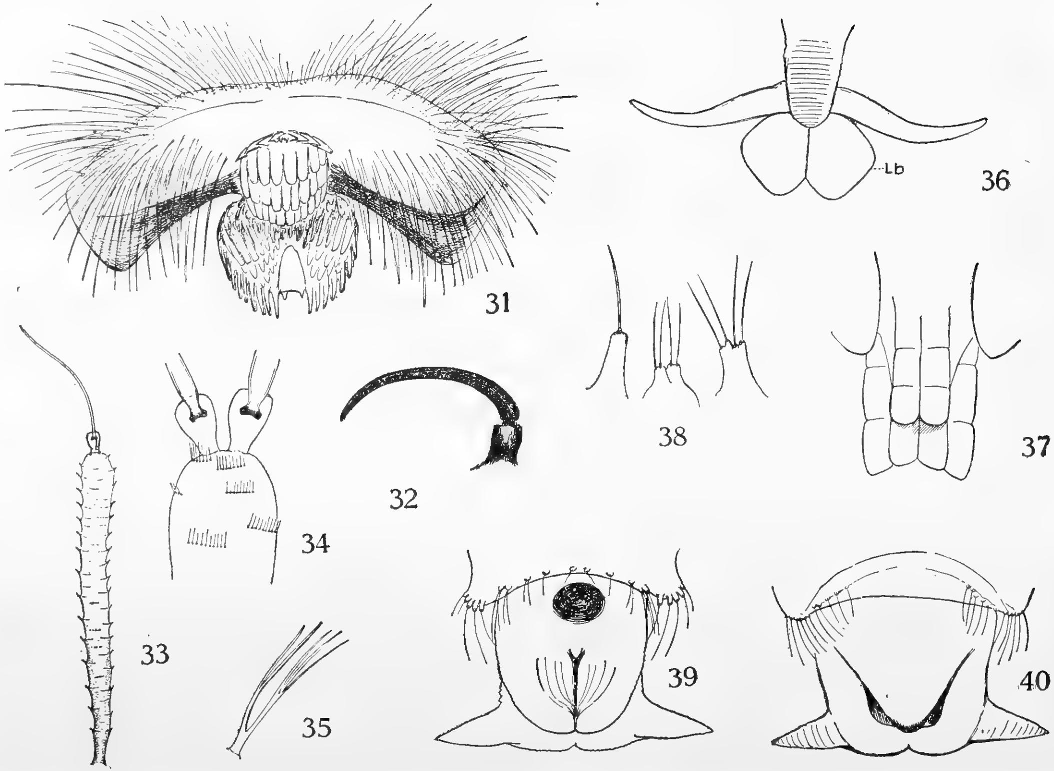
PTYCHOPTERA RUFOCINCTA

Larva: 16, head, dorsal aspect; 17, labium, ventral aspect; 18, antenna; 19, mandible and maxilla·



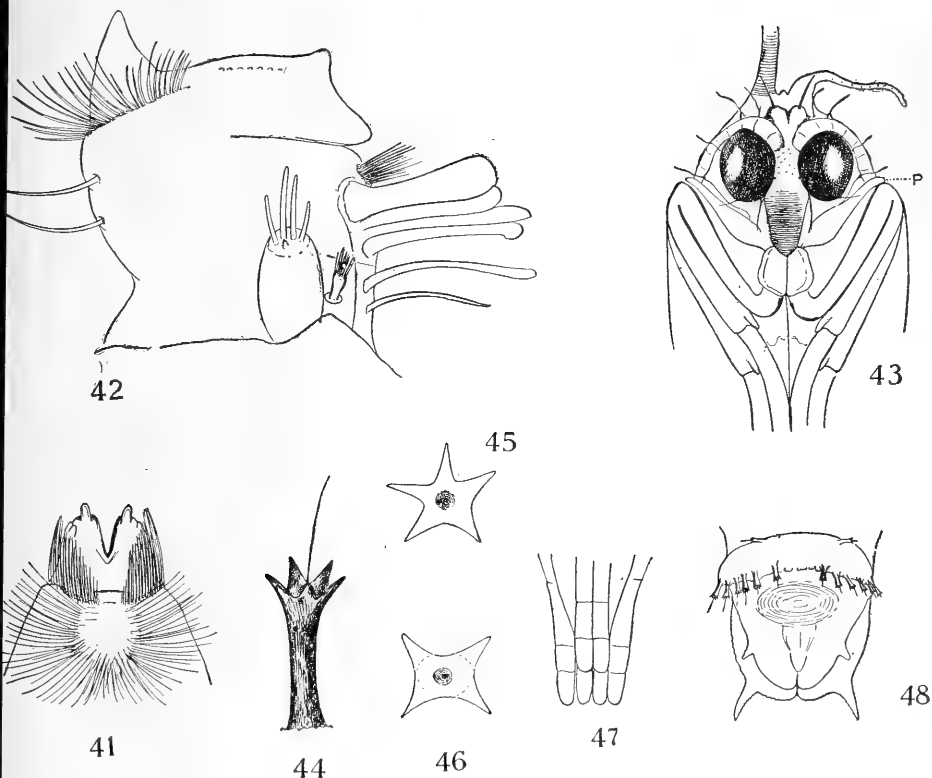
BITTACOMORPHELLA JONESI, LARVA

25, Dorsal aspect; 26, head, ventral aspect; 27, head, dorsal aspect; 28, labium, ventral aspect; 29, mandible and maxilla, ventral aspect; 30, mandible and antenna, dorsal aspect



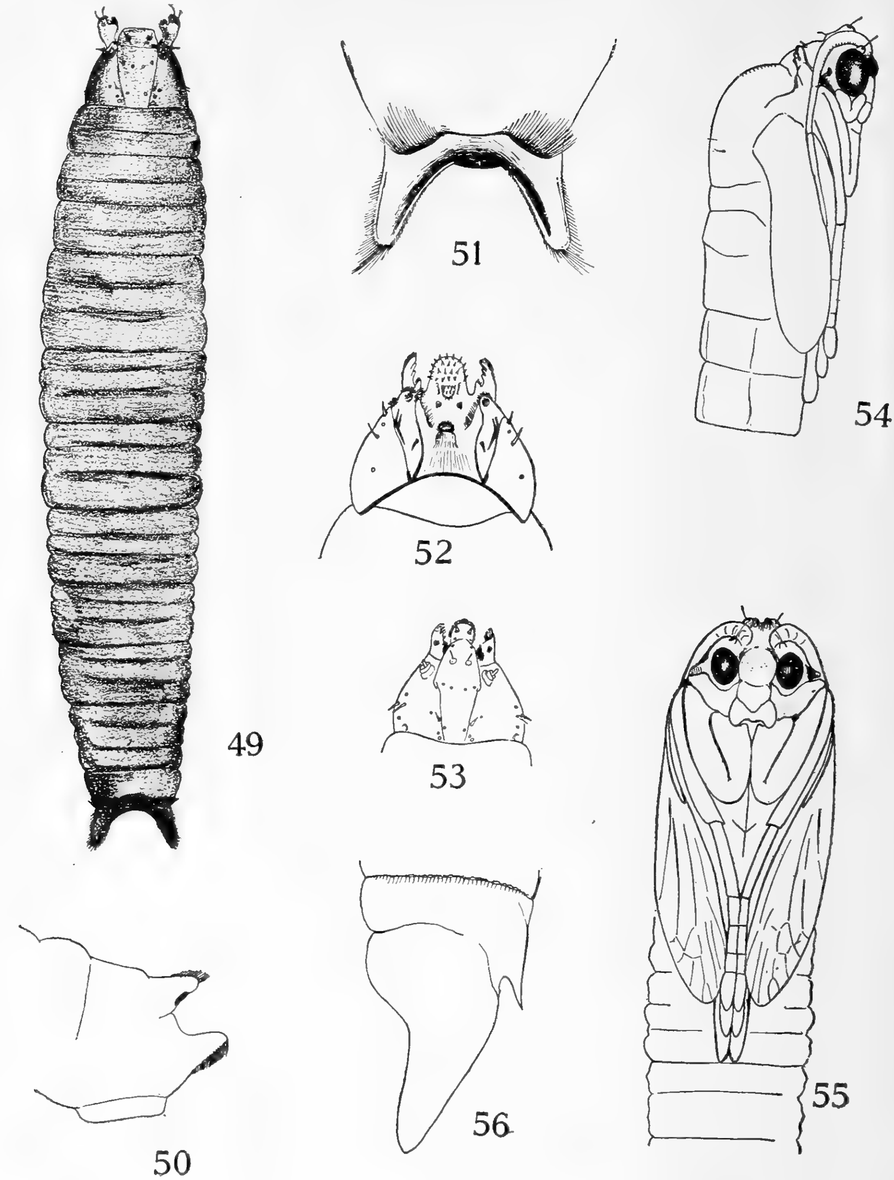
BITTACOMORPHELLA JONESI

Larva: 31, labrum-epipharynx; 32, apex of pseudopod, and claw; 33, body projection; 34, body projection, enlarged; 35, branched hairs on body



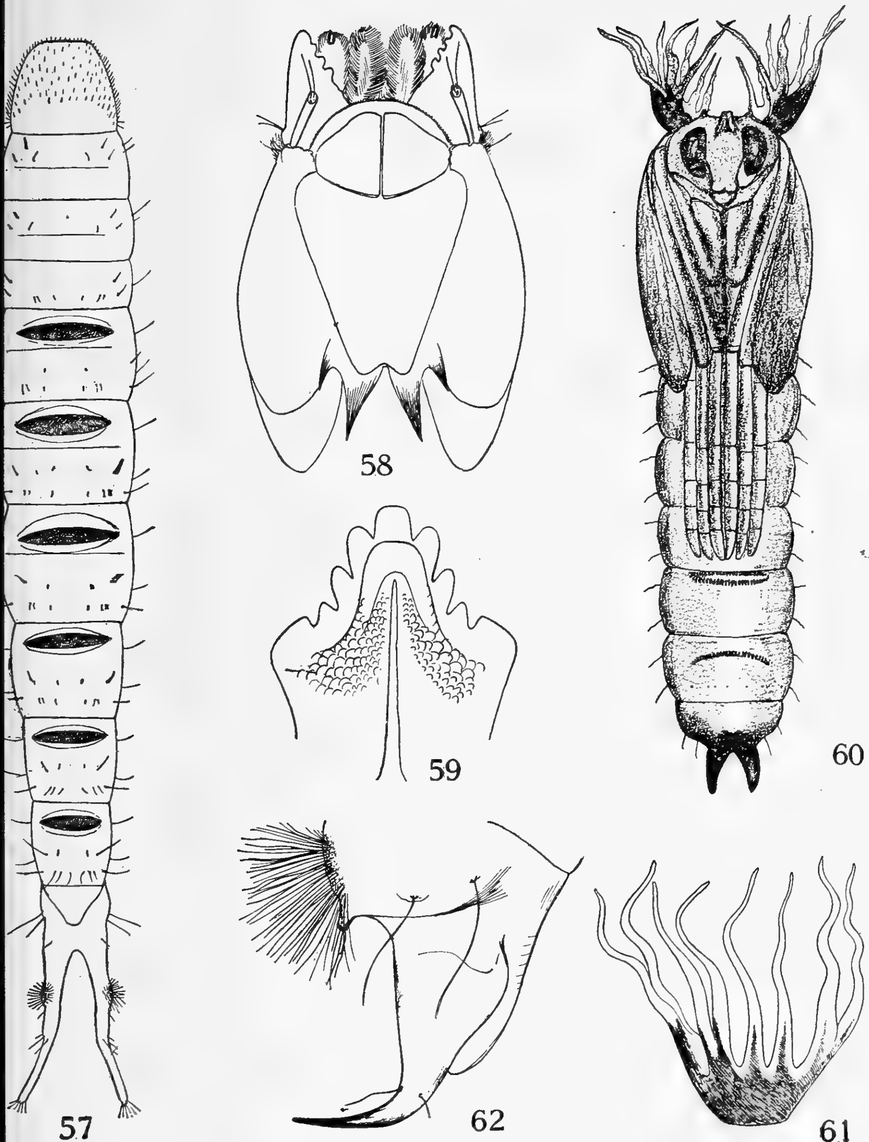
BITTACOMORPHA CLAVIPES

Larva: 41, labium; 42, mandible and antenna, dorsal aspect
Pupa: 43, ventral aspect; 44–46, types of abdominal tubercles; 47, arrangement of leg sheaths; 48, male cauda, dorsal aspect



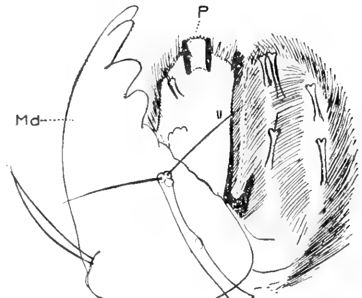
TRICHOCERA SP. (REGELATIONIS, SUPPOSITION)

Larva: 49, dorsal aspect; 50, spiracular disk, lateral aspect; 51, spiracular disk, dorsal aspect; 52, head, ventral aspect (after De Meijere); 53, head, dorsal aspect (after De Meijere)
Pupa: 54, lateral aspect; 55, female, ventral aspect; 56, female cauda, lateral aspect



ANTOCHA SAXICOLA

Larva: 57, dorsal aspect; 58, head capsule, dorsal aspect; 59, mentum
Pupa: 60, ventral aspect; 61, pronotal breathing horn, lateral aspect; 62, female cauda, teral aspect



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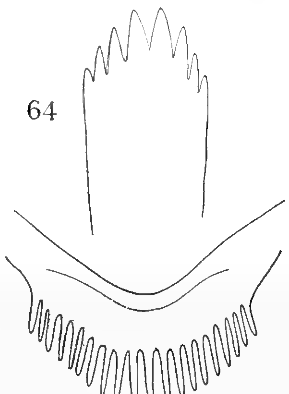

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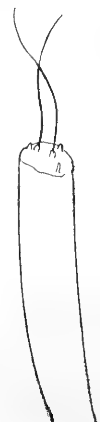

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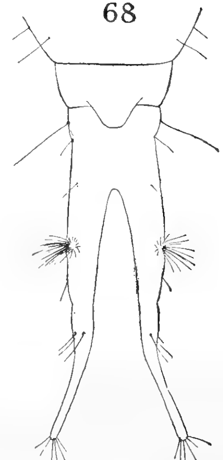

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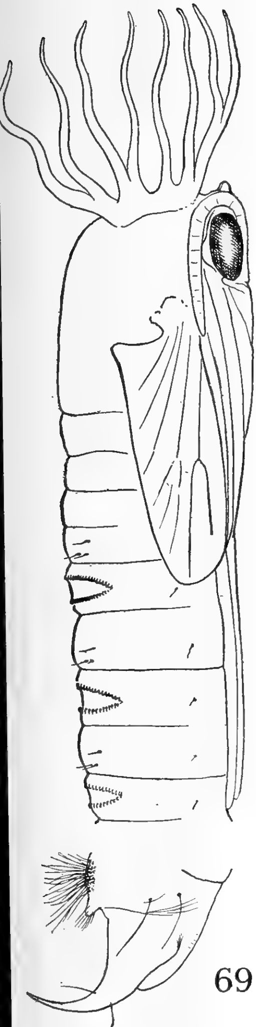
ANTOCHA SAXICOLA, LARVA



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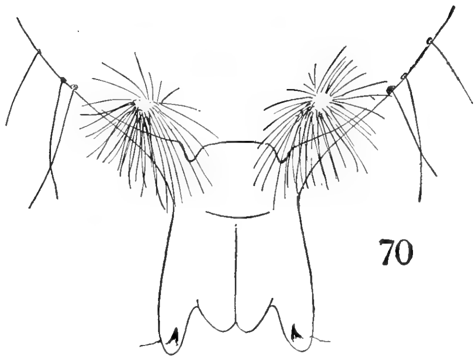

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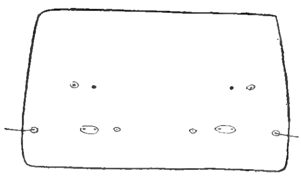
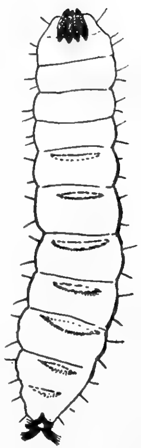


71

ANTOCHA SAXICOLA, PUPA

Lateral aspect; 70, male cauda, dorsal aspect; 71, fifth abdominal segment, dorsal aspect (diagrammatic)



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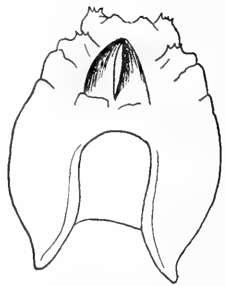

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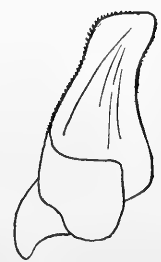

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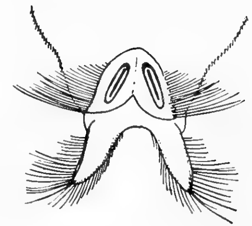

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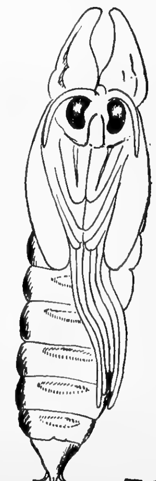

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Elliptera omissa (after Milk)

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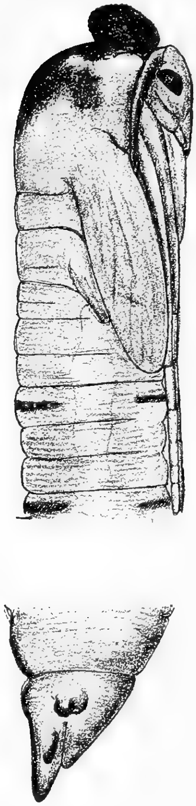

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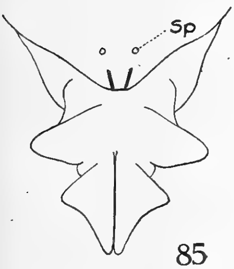

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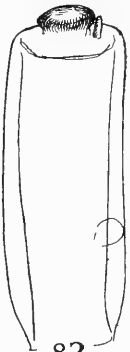

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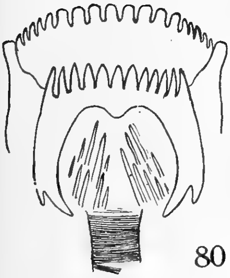

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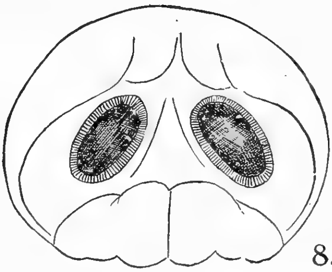
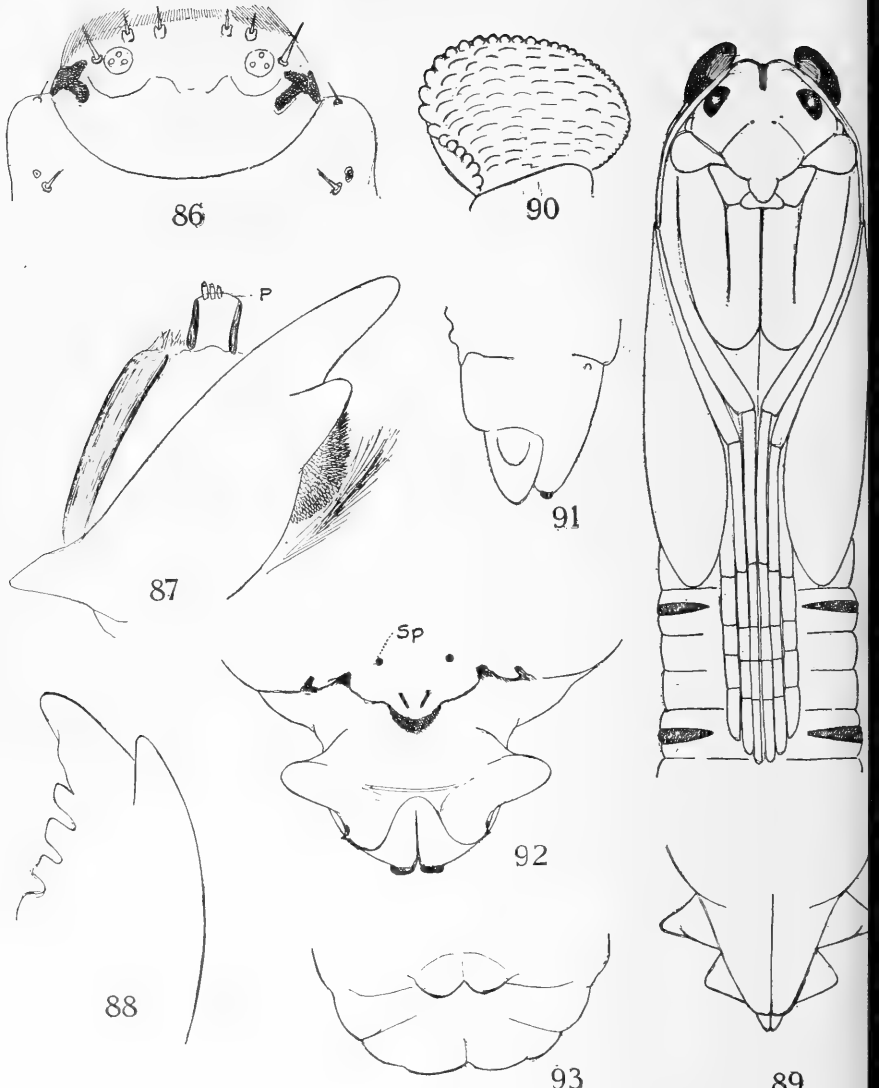


83

LIMNOBIA CINCTIPES

Larva: 79, head capsule, dorsal aspect; 80, hypopharynx; 81, mentum; 82, antenna; 83, spiracular disk

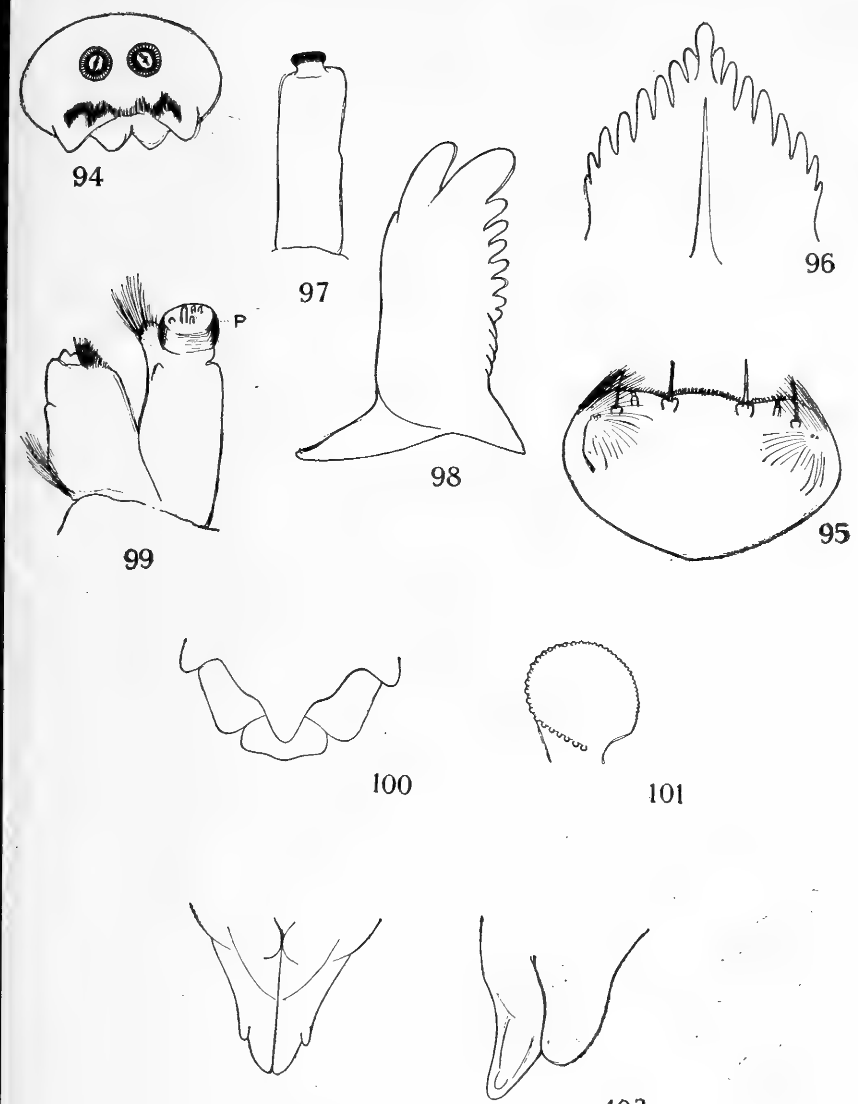
Pupa: 84, female, lateral aspect; 85, female cauda, dorsal aspect



LIMNOBIA CINCTIPES

Larva: 86, labrum-epipharynx; 87, mandible and maxilla; 88, mandible; 93, spiracula disk, dorsal aspect

Pupa: 89, female, ventral aspect; 90, pronotal breathing horn, lateral aspect; 91, ma cauda, lateral aspect; 92, male cauda, dorsal aspect



LIMNOBIA TRIOCELLATA AND L. FALLAX

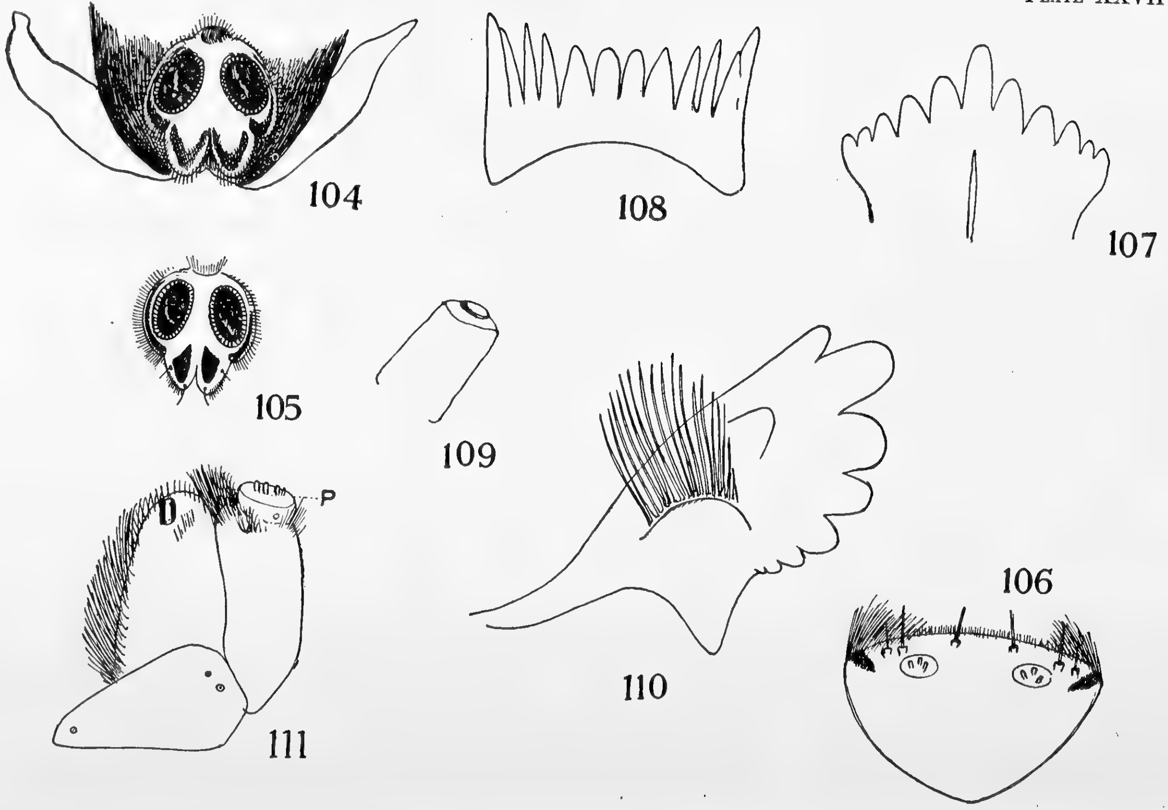
Limnobia triocellata: 94, spiracular disk

Limnobia fallax, larva: 95, labrum-epipharynx; 96, mentum; 97, antenna; 98, mandible; 99, maxilla

Limnobia fallax, pupa: 100, mouth parts; 101, pronotal breathing horn; 102, female cauda, dorsal aspect; 103, female cauda, lateral aspect

Memoir 38

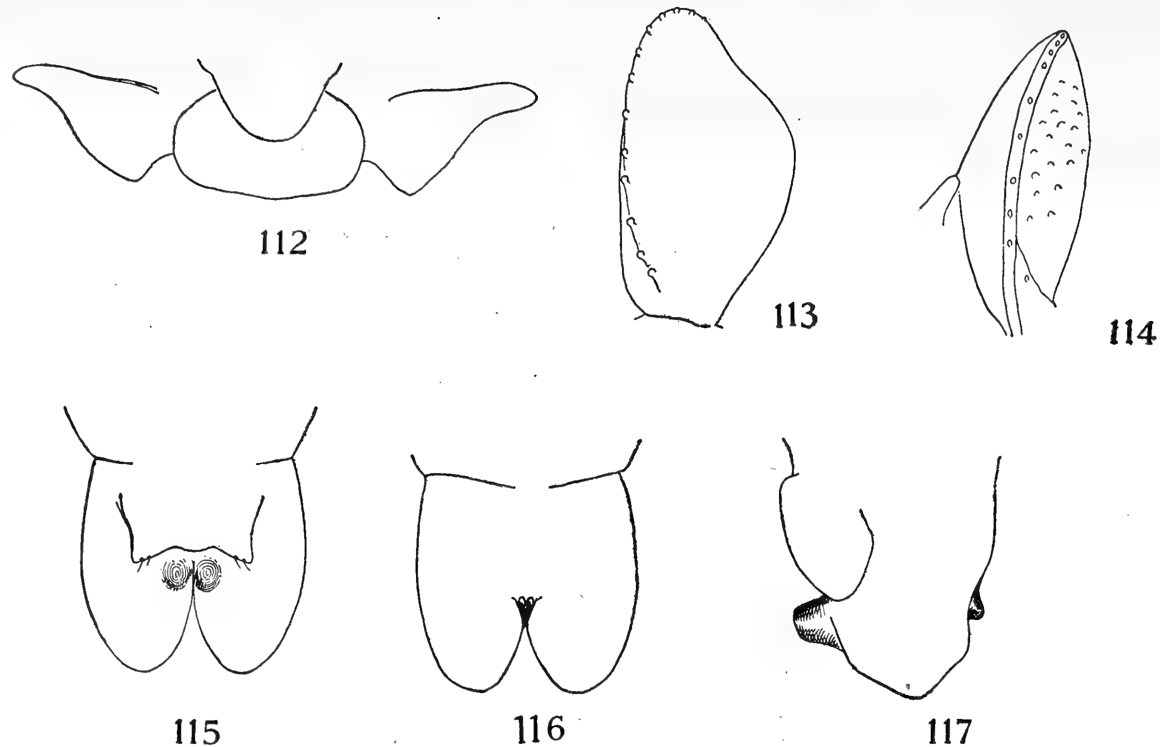
Plate XXVII



DICRANOMYIA BADIA AND D. STULTA

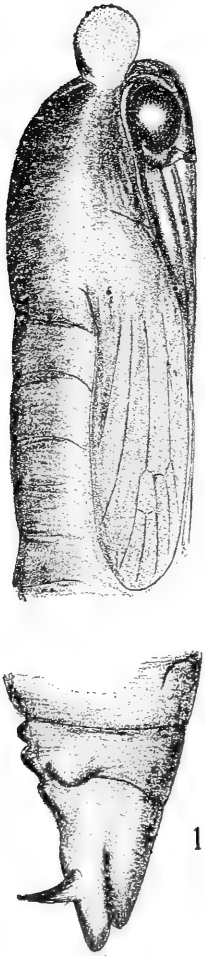
Dicranomyia badia: 104, spiracular disk

Dicranomyia stulta, larva: 105, spiracular disk; 106, labrum; 107, mentum; 108, hypopharynx; 109, antenna; 110, mandible; 111, maxilla



DICRANOMYIA STULTA, PUPA

112, Mouth parts; **113**, pronotal breathing horn, dorsal aspect; 114, pronotal breathing horn, lateral aspect; 115, male cauda, dorsal aspect; 116, male cauda, ventral aspect; 117, male cauda, lateral aspect



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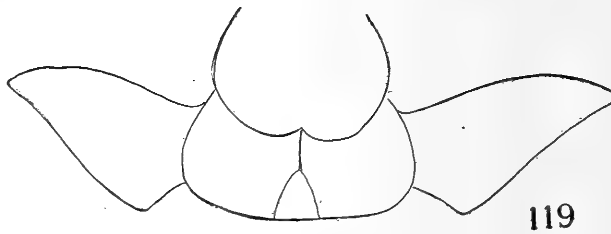

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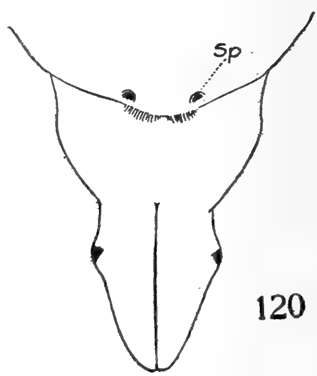

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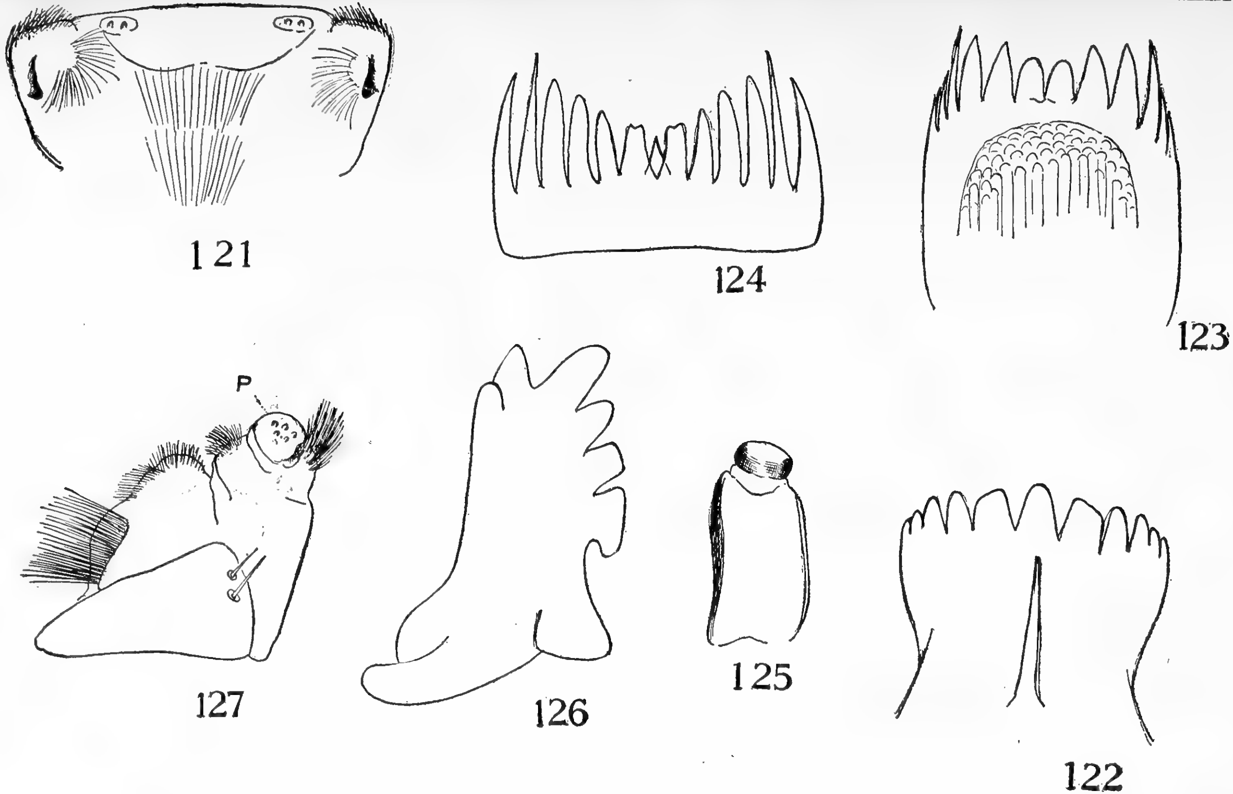
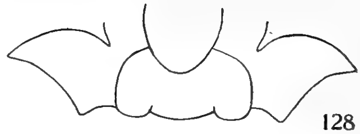
DICRANOMYIA BADIA, PUPA

118, Lateral aspect; 119, mouth parts; 120, female cauda, dorsal aspect



RHIPIDIA BRYANTI, LARVA

121, Labrum-epipharynx; 122, mentum; 123 and 124, hypopharynx; 125, antenna; 126, mandible; 127, maxilla



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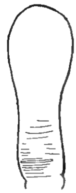

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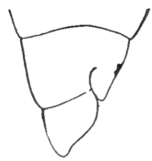

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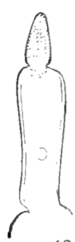

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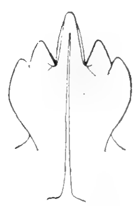

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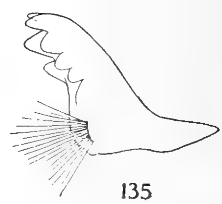

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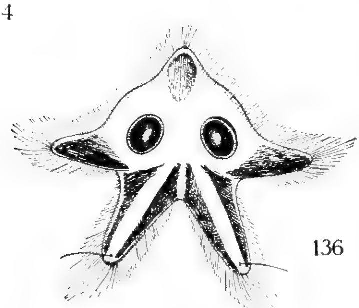


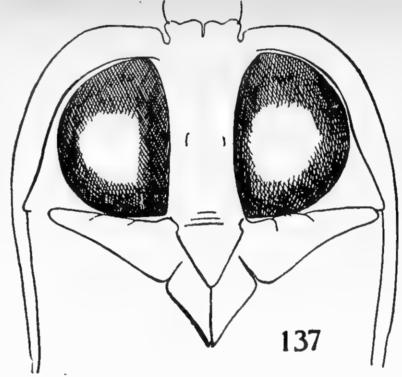
136

RHIPIDIA BRYANTI, RHAMPHIDIA MAINENSIS, AND RHAMPHIDIA FLAVIPES

Rhipidia bryanti, pupa: 128, mouth parts; 129, pronotal breathing horn; 130, male cauda, lateral aspect; 131, male cauda, dorsal aspect

Rhamphidia mainensis, larva: 132, lateral aspect; 133, mentum; 135, mandible; 136, spiracular disk

Rhamphidia flavipes, larva: 134, antenna



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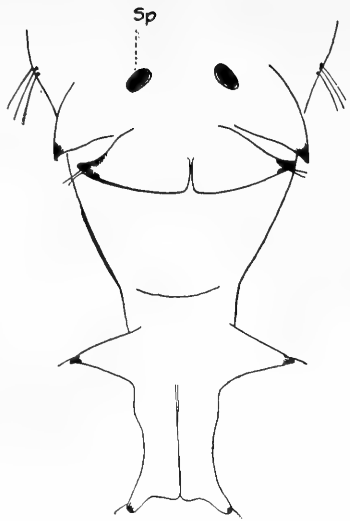

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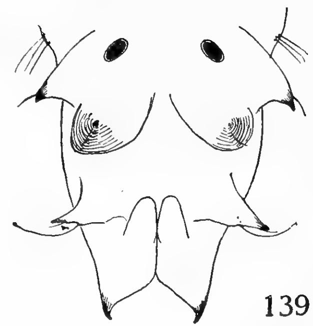

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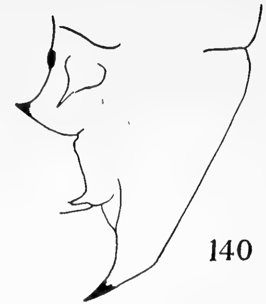

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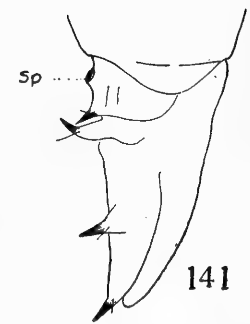
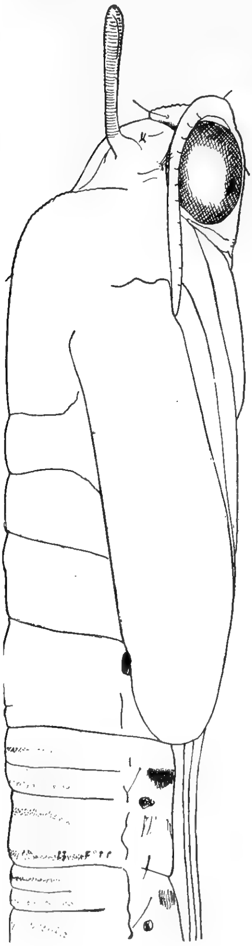


141

RHAMPHIDIA FLAVIPES, PUPA

137, Head of male, ventral aspect; 138, female cauda, dorsal aspect; 139, male cauda, dorsal aspect; 140, male cauda, lateral aspect; 141, female cauda, lateral aspect



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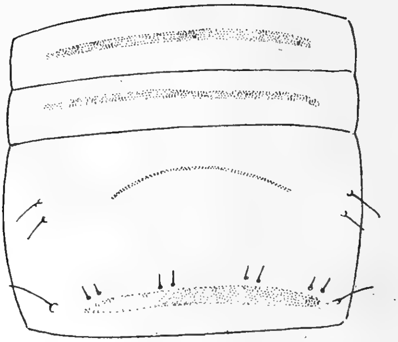

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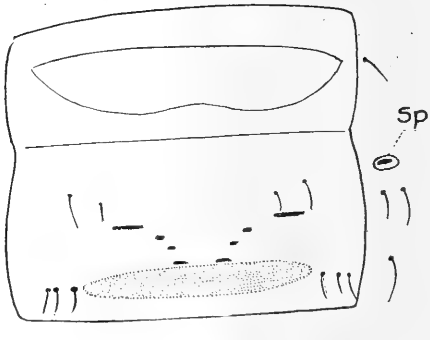
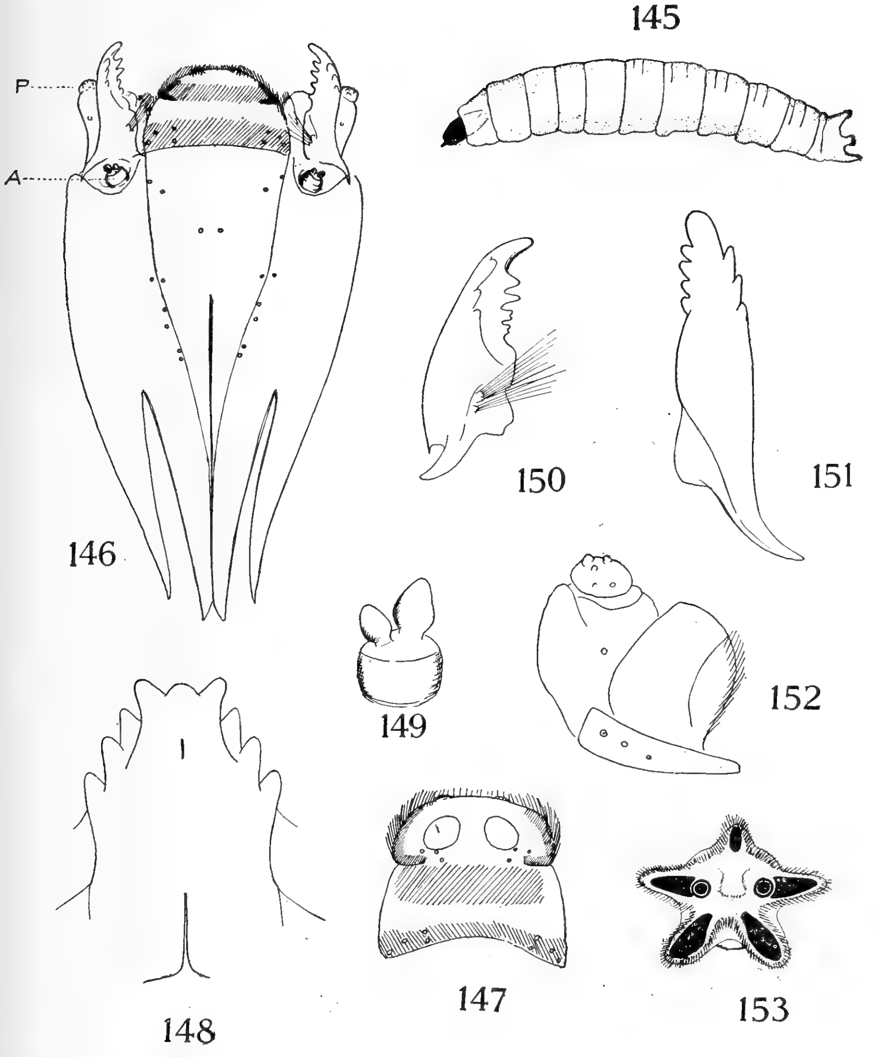


14

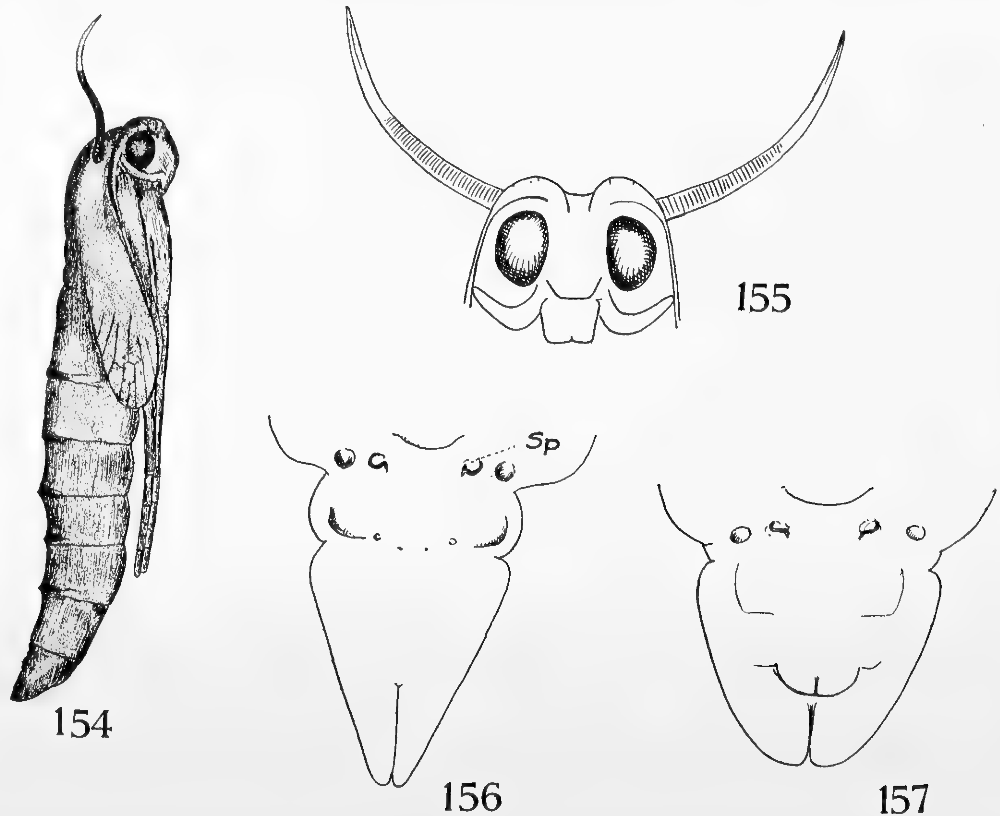
RHAMPHIDIA FLAVIPES, PUPA

142, Lateral aspect; 143, fifth abdominal segment, dorsal aspect (diagrammatic); 1
fifth abdominal segment, ventral aspect (diagrammatic)



ULA ELEGANS, LARVA

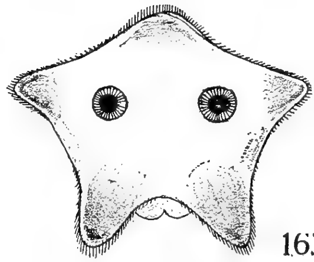
145, Lateral aspect; 146, head capsule, dorsal aspect; 147, labrum-epipharynx; 148, mentum 149, antenna; 150, mandible, lateral aspect; 151, mandible, from inside; 152, maxilla; 153, spiracular disk



ULA ELEGANS, PUPA

154, Female, lateral aspect; 155, head, ventral aspect; 156, female cauda, dorsal aspect; 157, male

158



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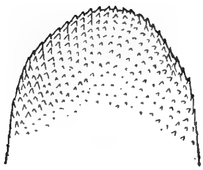

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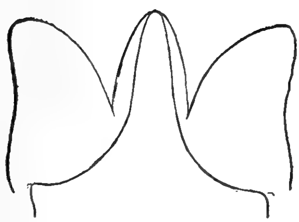

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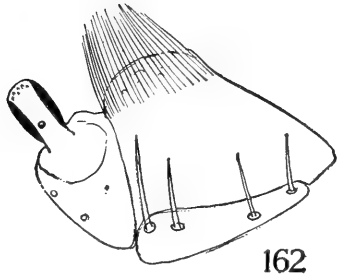
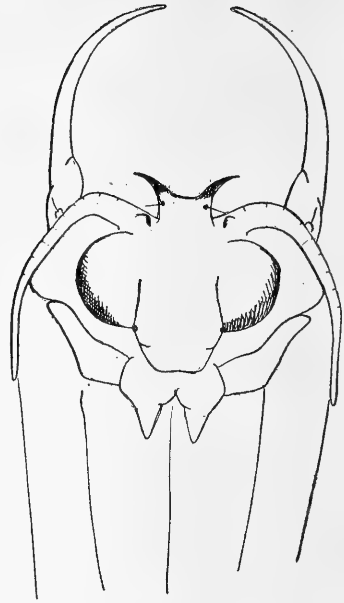


162

EPIPHRAGMA SOLATRIX, LARVA

158, Head capsule, ventral aspect; 159, mentum; 160, prementum; 161, hypopharynx; 162, maxilla; 163, spiracular disk

164



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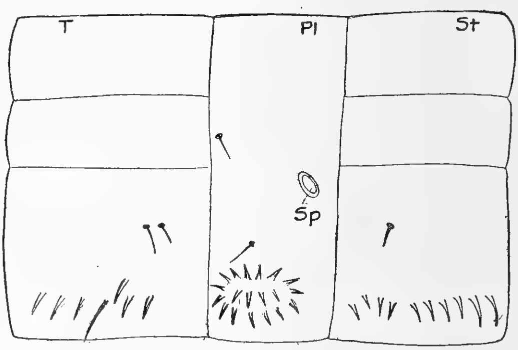


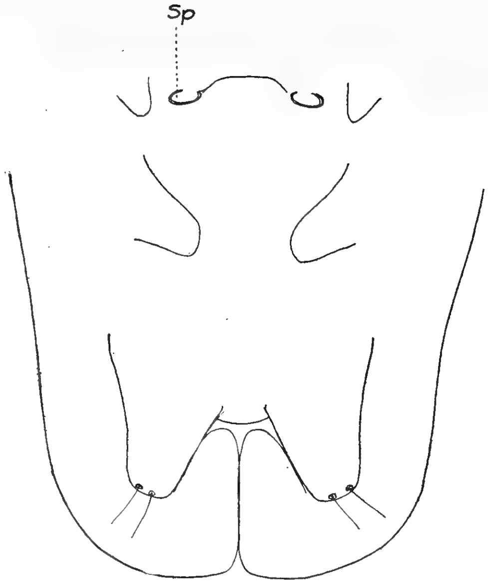
165

167

EPIPHRAGMA SOLATRIX AND E. FASCIPENNIS

Epiphragma solatrix, pupa: 164, lateral aspect; 166, head of male, ventral aspect; 167, fifth abdominal segment (diagrammatic)

Epiphragma fascipennis, pupa: 165, cephalic crest, lateral aspect



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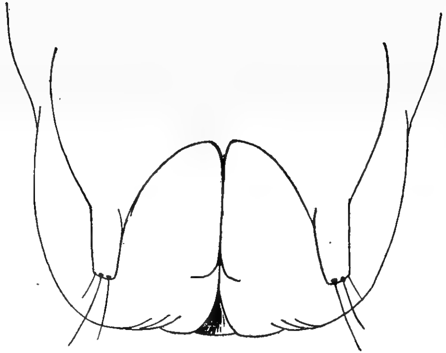

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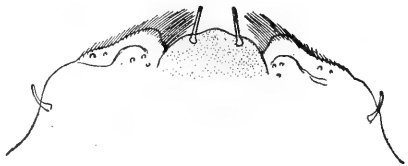

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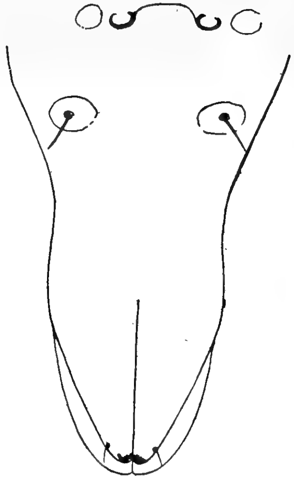
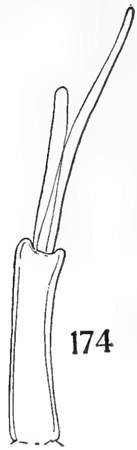


171

EPIPHRAGMA FASCIPENNIS AND E. SOLATRIX

Epiphragma fascipennis: 168, larva, labrum; 169, pupa, male cauda, dorsal aspect
Epiphragma solatrix, pupa: 170, male cauda, dorsal aspect; 171, female cauda, dorsal aspect



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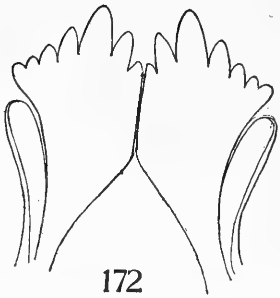

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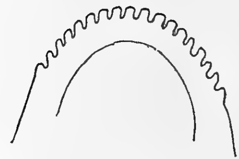

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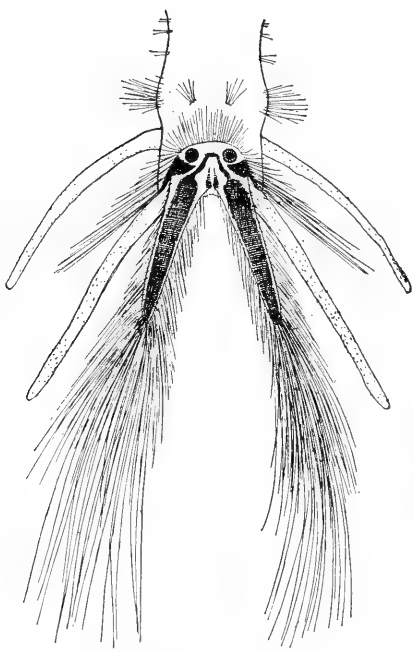

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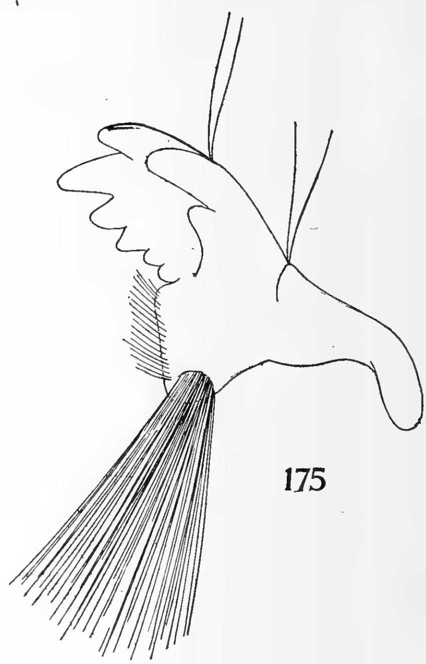
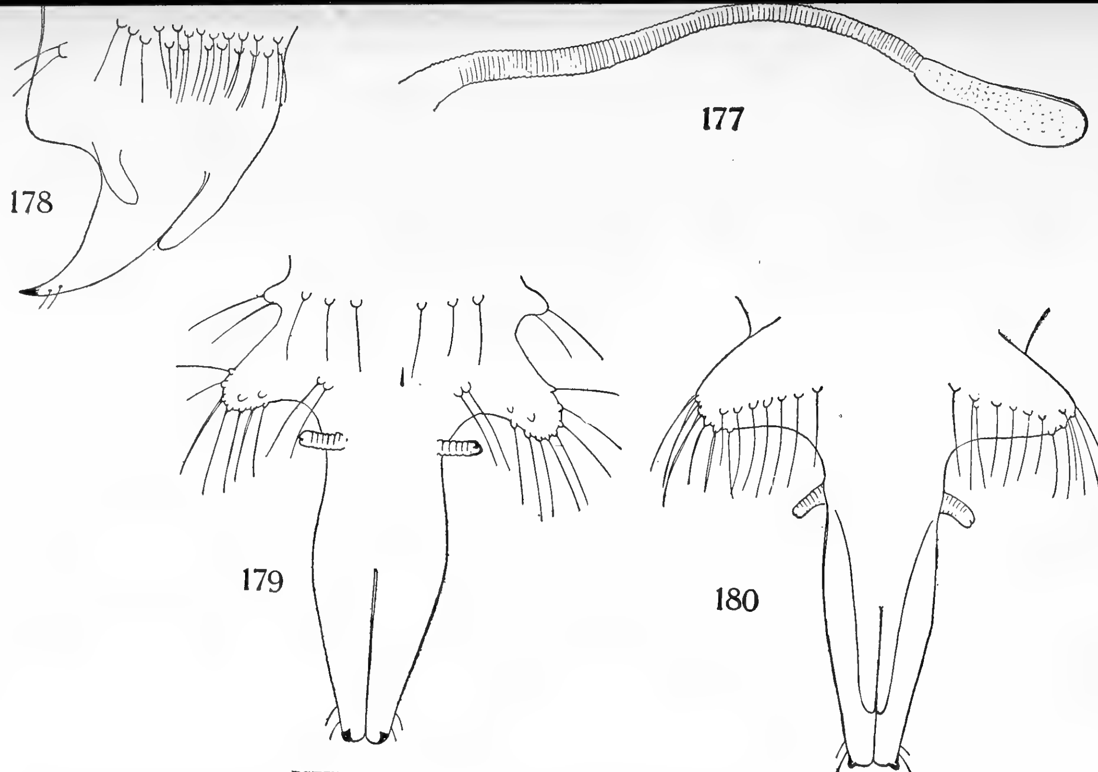


175

PSEUDOLIMNOPHILA LUTEIPENNIS AND P. INORNATA

Pseudolimnophila luteipennis, larva: 172, mentum; 173, hypopharynx; 175, mandible; 176, spiracular disk

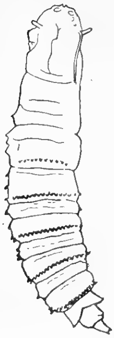
Pseudolimnophila inornata, larva: 174, antenna



PSEUDOLIMNOPHILA INORNATA AND P. LUTEIPENNIS

Pseudolimnophila inornata, pupa: 177, pronotal breathing horn

Pseudolimnophila luteipennis, pupa: 178, male cauda, lateral aspect; 179, female cauda, dorsal aspect; 180, female cauda, ventral aspect



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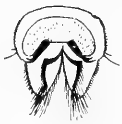

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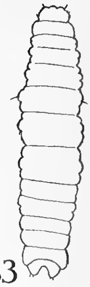

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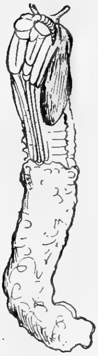

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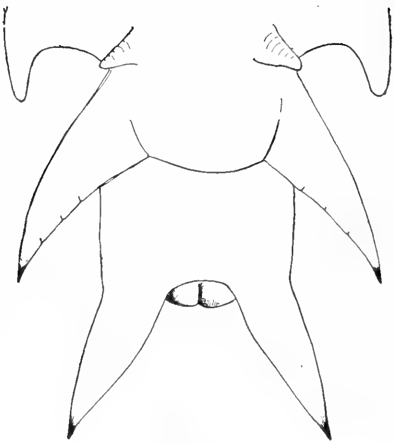

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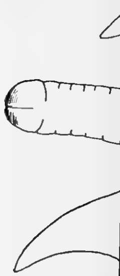
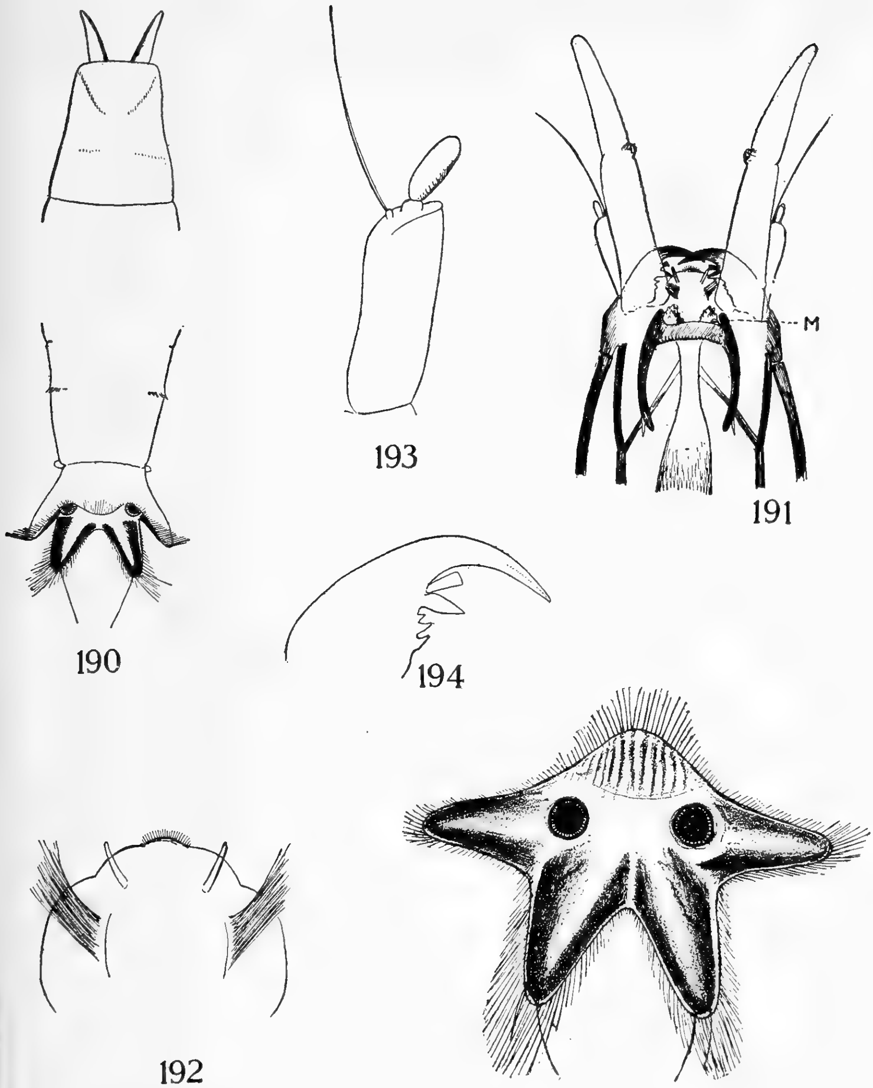


DACTYLOLABIS DENTICULATA, D. WODZICKII, AND D. CUBITALIS

Dactylolabis denticulata (after Mik): 181, pupa; 182, larva, head capsule, ventral 183, larva, dorsal aspect

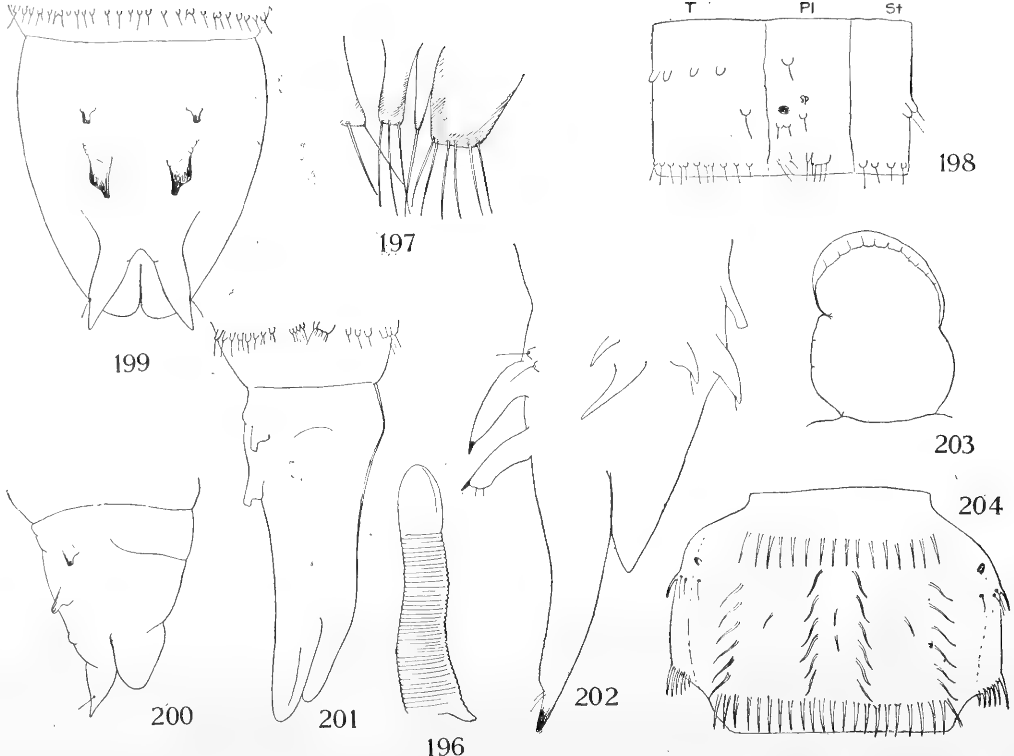
Dactylolabis wodzickii (after Nowicki): 184, pupa; 185, larva, head capsule; 18 spiracular disk

Dactylolabis cubitalis, pupa: 187, pronotal breathing horn; 188, second abdomi ment, showing spiracle; 189, male cauda, dorsal aspect



LIMNOPHILA (DICRANOPHRAGMA) FUSCOVARIA, LARVA

190, Cephalic and caudal ends, dorsal aspect; 191, head capsule, ventral aspect; 192, labrum epipharynx; 193, antenna; 194, mandible; 195, spiracular disk

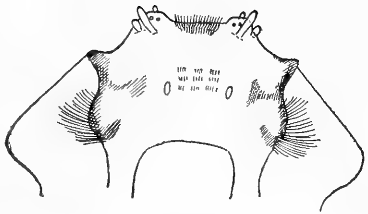


LIMNOPHILA (DICRANOPHRAGMA) FUSCOVARIA AND LIMNOPHILA (PHYLIDOREA) ADUSTA, SUPPOSITION

Limnophila (*Dicranophragma*) *fuscovaria*, pupa: 196, pronotal breathing horn; 197, pleural abdominal spines; 198, fifth abdominal segment (diagrammatic); 199, male cauda, dorsal aspect; 200, male cauda, lateral aspect; 201, female cauda, lateral aspect

Limnophila (*Phylidorea*) *adusta* (supp.), pupa: 202, female cauda, lateral aspect; 203, pronotal breathing horn; 204, fifth abdominal segment, ventral aspect

207



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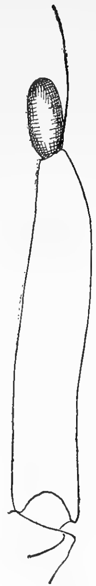

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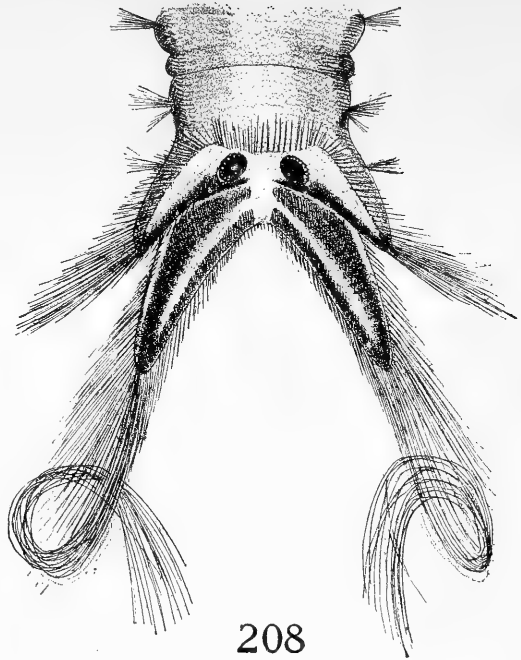
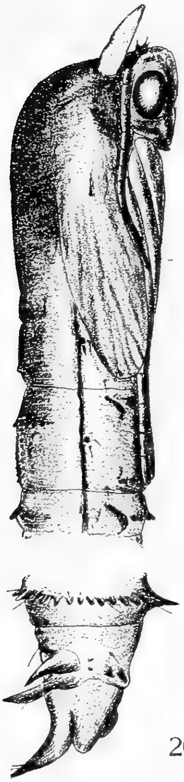


208

LIMNOPHILA (LASIOMASTIX) MACROCERA, LARVA

205, Labrum; 206, antenna; 207, mandible; 208, spiracular disk, dorsal aspect



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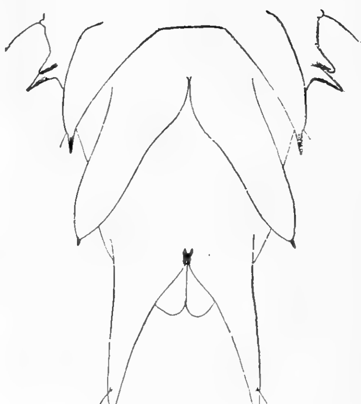

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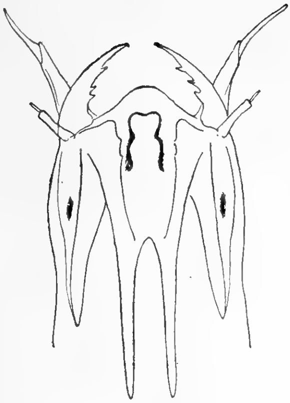
LIMNOPHILA (LASIOMASTIX) MACROCERA, PUPA

209, Male, lateral aspect; 210, mouth parts; 211, male cauda, dorsal aspect; 212, fem
cauda, lateral aspect



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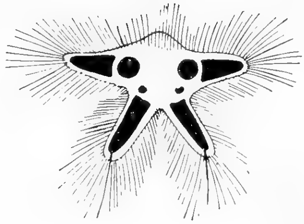

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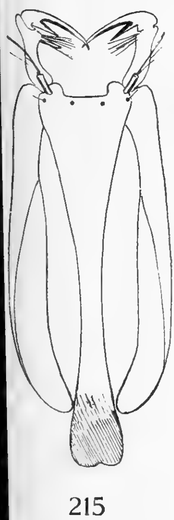

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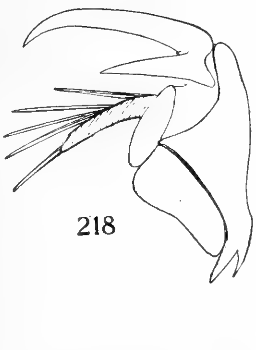

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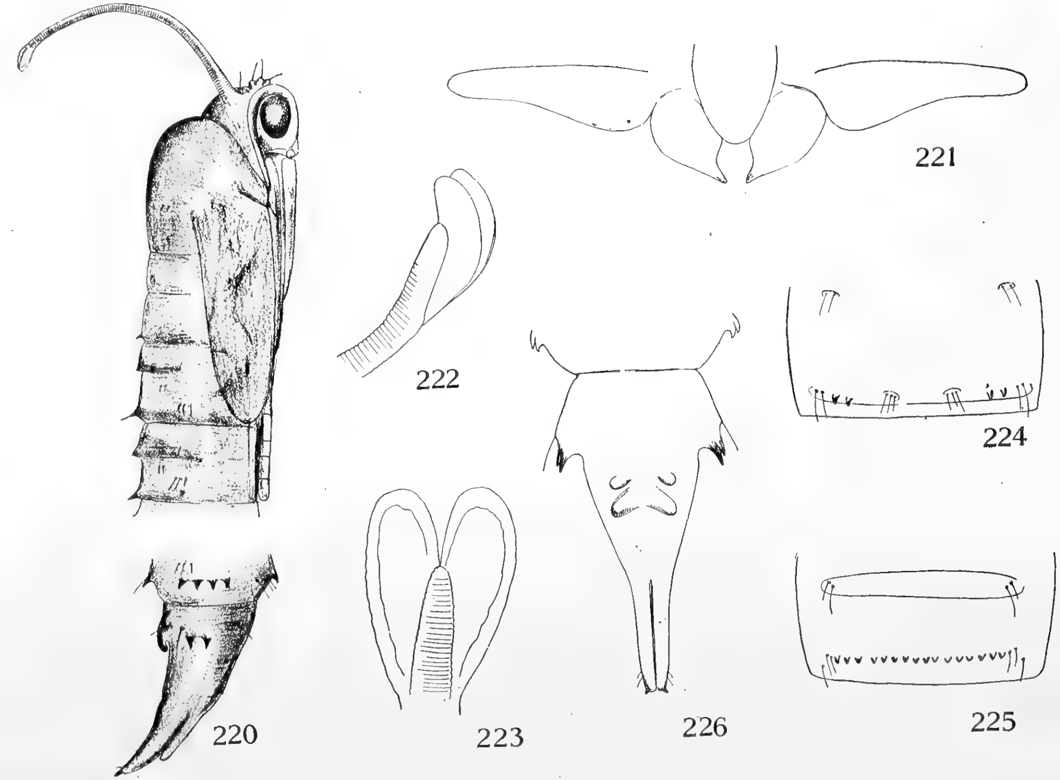
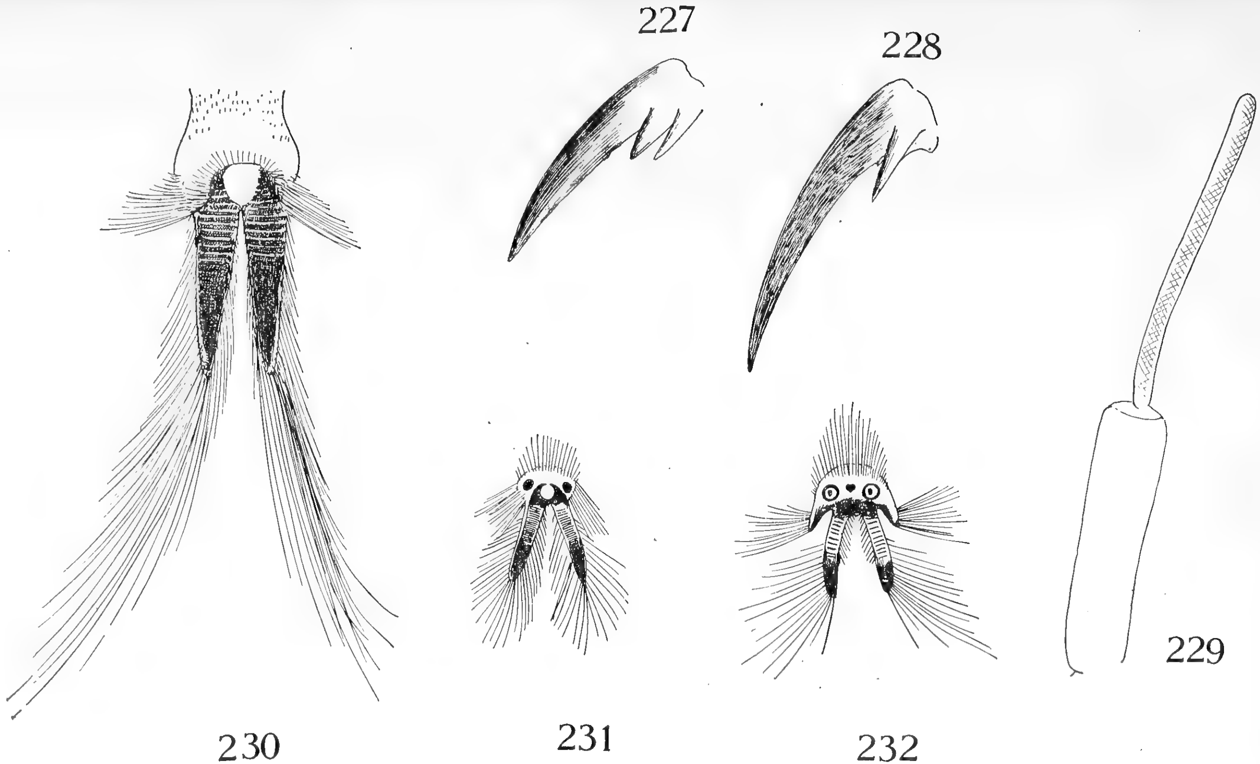
LIMNOPHILA PICTIPENNIS, L. PUNCTATA, AND ULOMORPHA PILOSELLA

Limnophila pictipennis: 213, head capsule (after Brauer)
Limnophila punctata: 214, spiracular disk (after Gerbig)
Ulomorpha pilosella, larva: 215, head capsule, dorsal aspect; 216, labrum; 217, antenna; 218, mandible; 219, spiracular disk, dorsal aspect



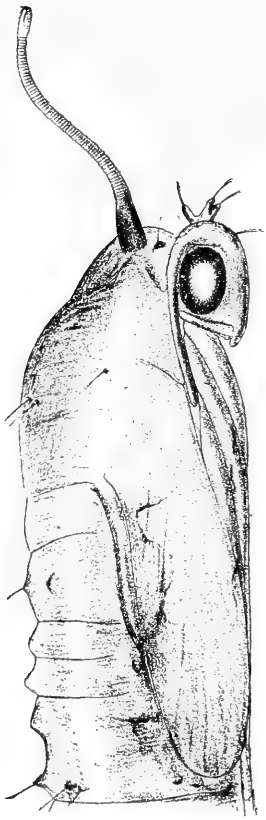
ULOMORPHA PILOSELLA, PUPA

220. Female, lateral aspect; 221, mouth parts; 222, apex of breathing horn; 223, apex of breathing horn



PILARIA RECONDITA, P. TENUIPES, P. FUSCIPENNIS, AND P. DISCICOLLIS

Pilaria recondita, larva: 227, tip of mandible
Pilaria tenuipes, larva: 228, tip of mandible; 229, antenna; 230, spiracular disk, dorsal aspect
Pilaria fuscipennis: 231, spiracular disk (after Gerbig)
Pilaria discicollis: 232, spiracular disk (after Gerbig)



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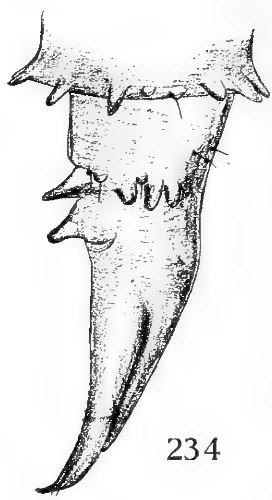

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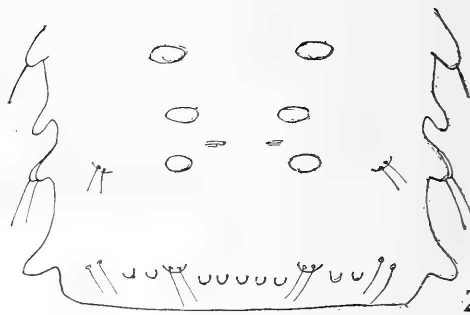

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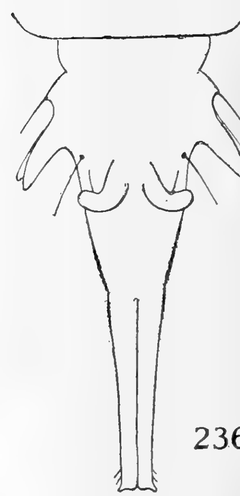
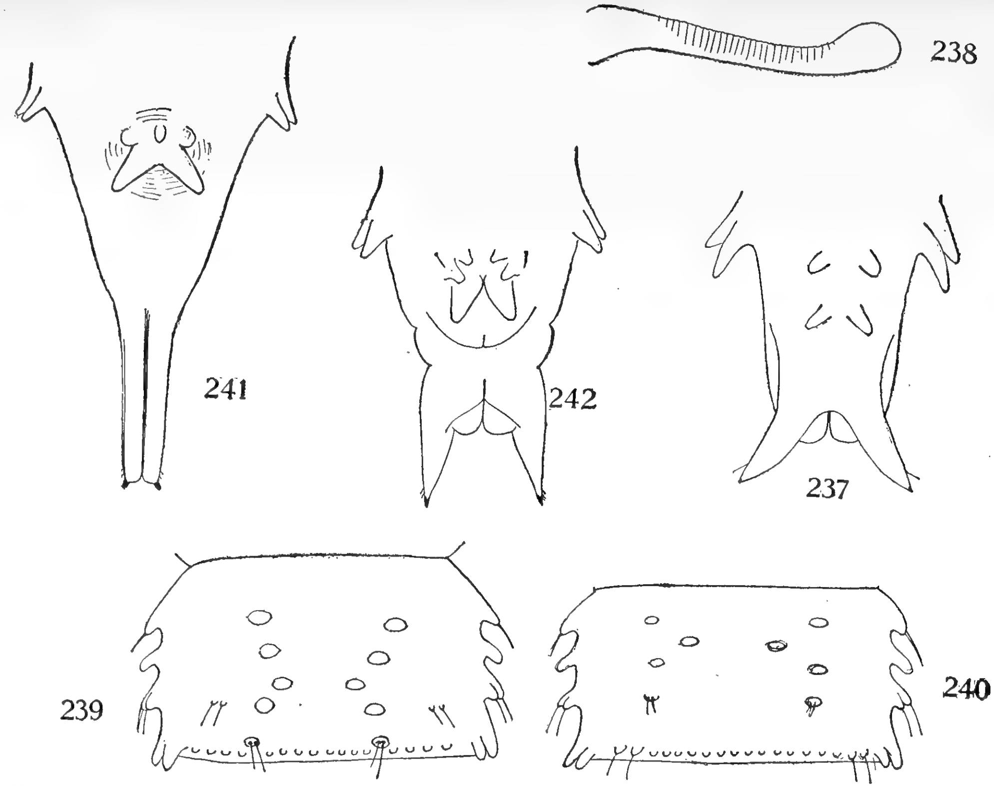


236

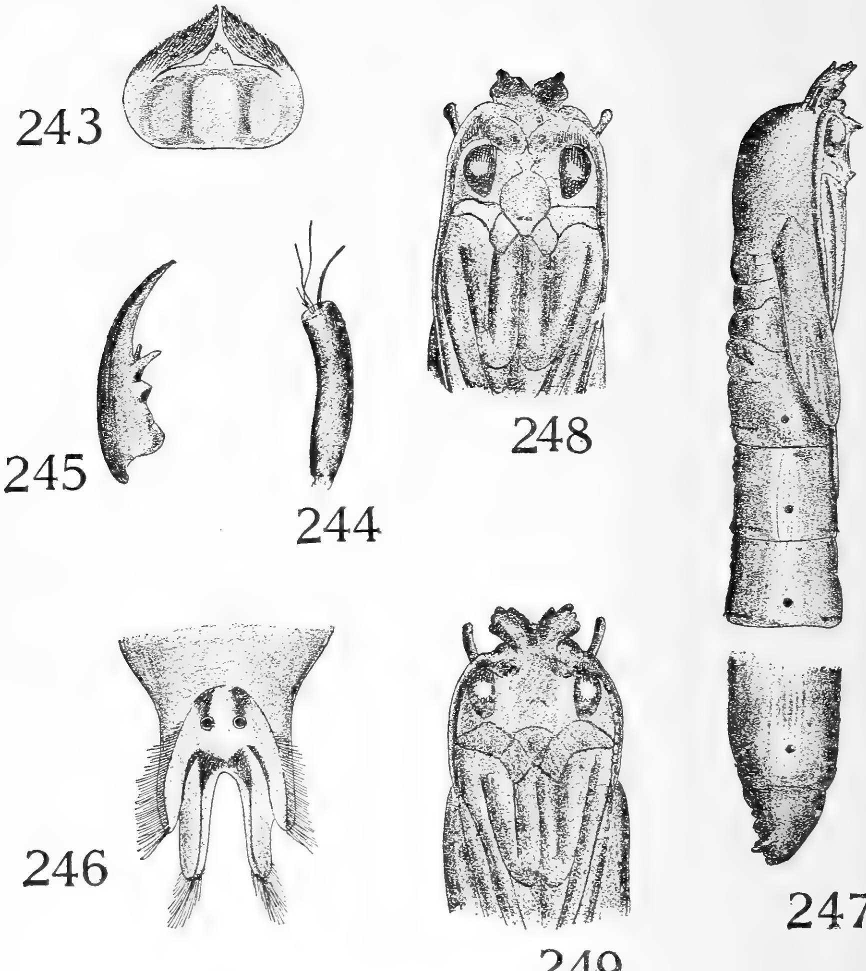
PILARIA TENUIPES, PUPA

233, Female, lateral aspect; 234, female cauda, lateral aspect; 235, fifth abdominal segment, dorsal aspect; 236, female cauda, dorsal aspect



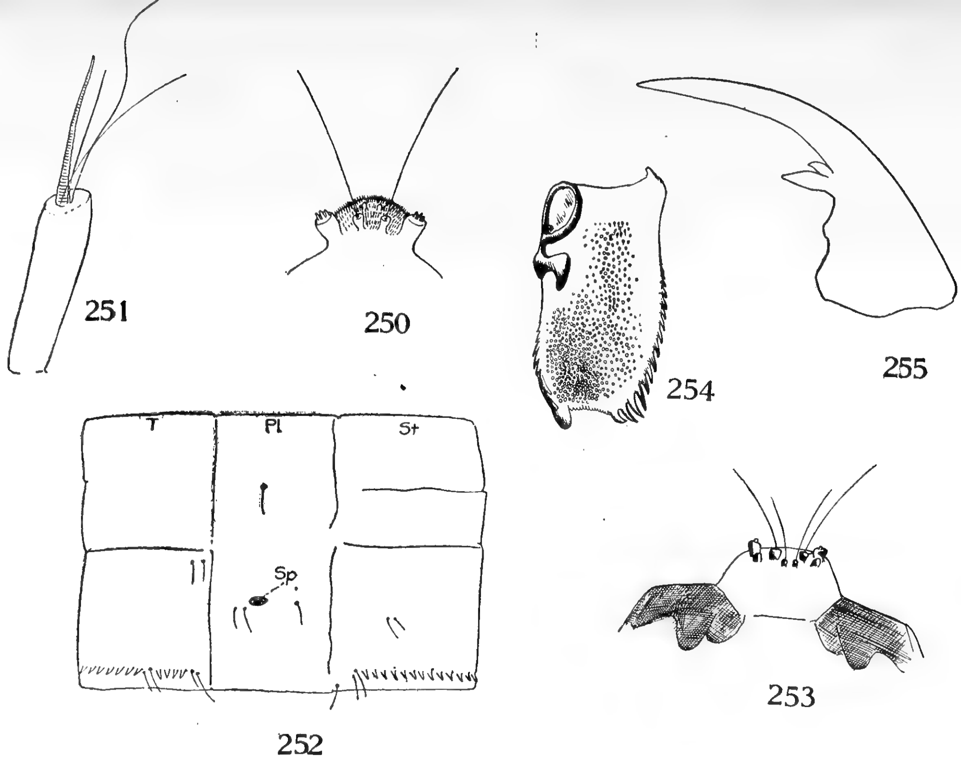
PILARIA RECONDITA AND P. QUADRATA

Pilaria recondita, pupa: 237, male cauda, dorsal aspect
Pilaria quadrata, pupa: 238, pronotal breathing horn; 239, fifth abdominal segment, dorsal aspect; 240, fifth abdominal segment, ventral aspect; 241, female cauda, dorsal aspect; 242, male cauda, dorsal aspect



HEXATOMA MEGACERA

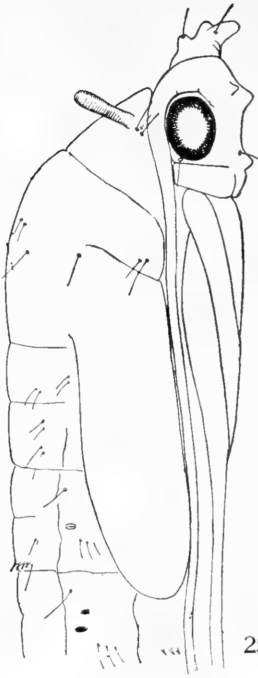
Larva: 243, labrum; 244, antenna; 245, mandible; 246, spiracular disk
Pupa: 247, lateral aspect; 248, male, ventral aspect; 249, female, ventral aspect



HEXATOMA MEGACERA AND ERIOCERA CINEREA

Hexatoma megacera: 250, larva, apex of labrum; 251, larva, antenna; 252, pupa, fifth abdominal segment, lateral aspect

Eriocera cinerea, larva: 253, labrum; 254, pharyngeal plate; 255, mandible



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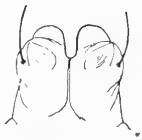

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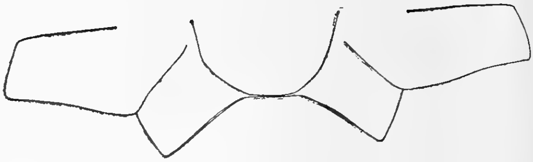

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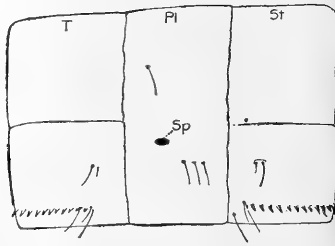

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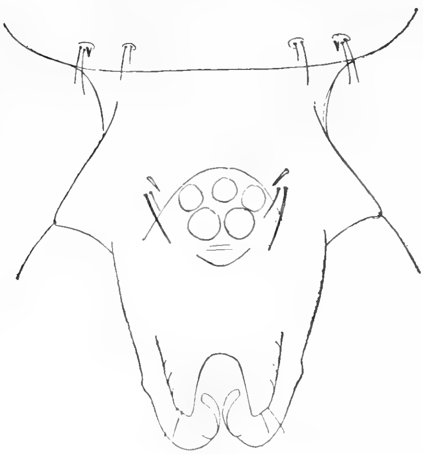

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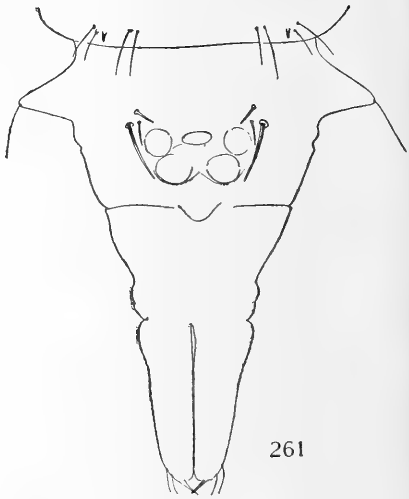
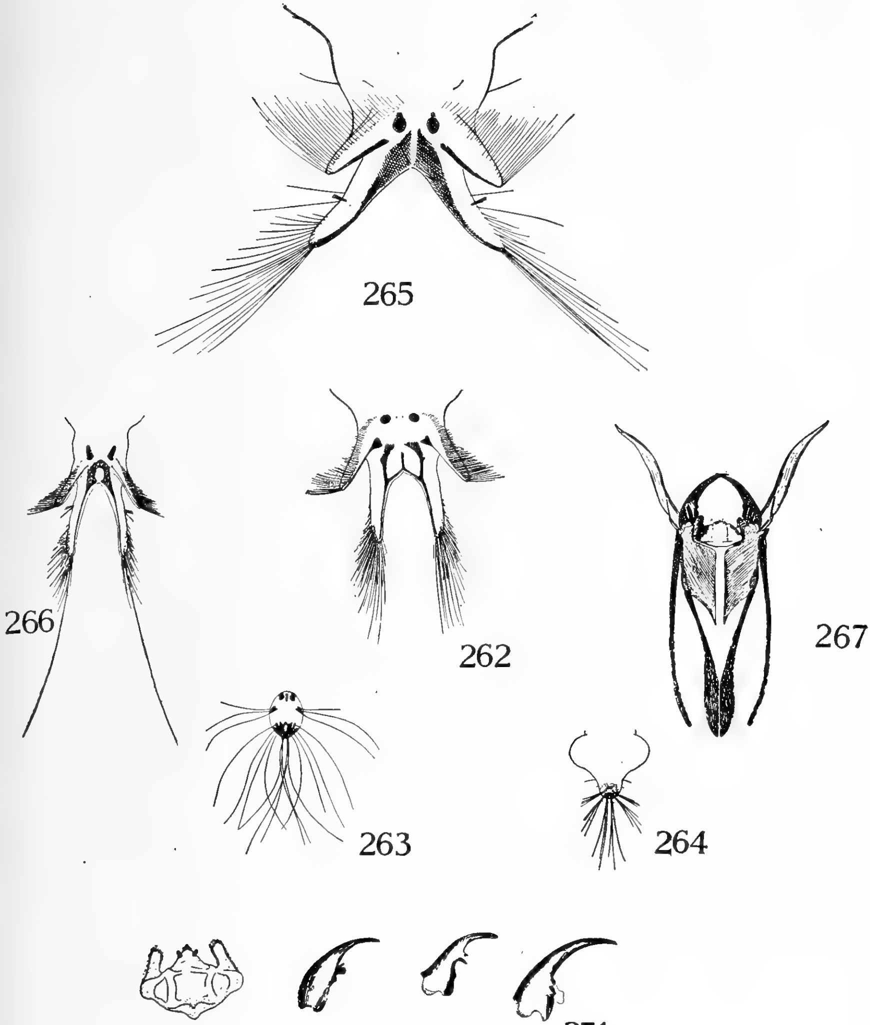


261

ERIOCERA CINEREA, PUPA

256, Male, lateral aspect; 257, cephalic crest of male, ventral aspect; 258, mouth parts; 259, fifth abdominal segment, lateral aspect; 260, male cauda, dorsal aspect; 261, female cauda, dorsal aspect



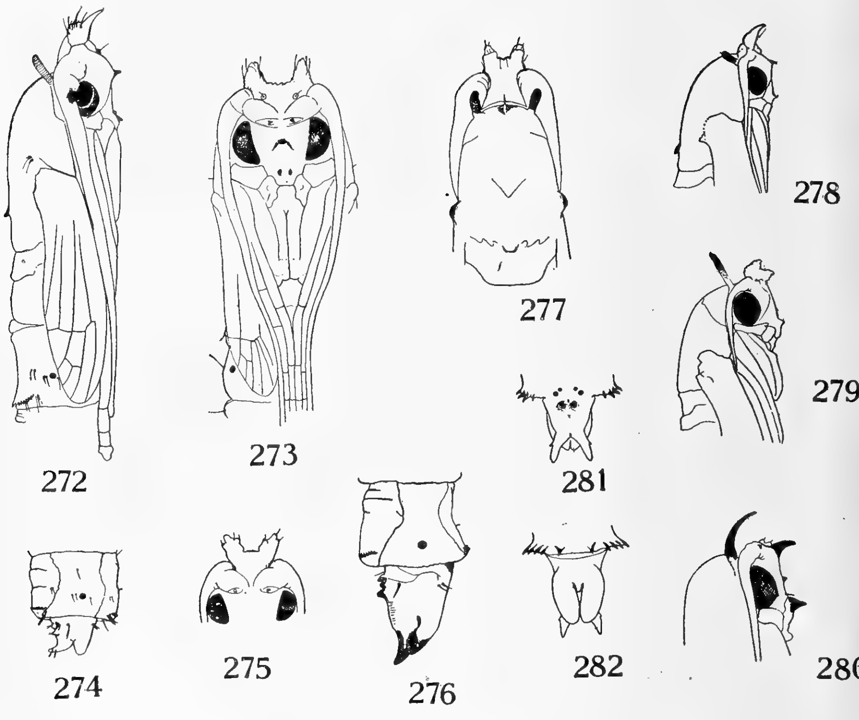
ERIOCERA SPINOSA, E. CINEREA, E. LONGICORNIS, AND E. FULTONENSIS

Eriocera spinosa, larva: 262, spiracular disk; 267, head capsule, dorsal aspect; 271, mandible

Eriocera cinerea, larva: 263 and 264, spiracular disk; 270, mandible

Eriocera longicornis, larva: 265, spiracular disk

Eriocera fultonensis, larva: 266, spiracular disk; 268, labrum; 269, mandible

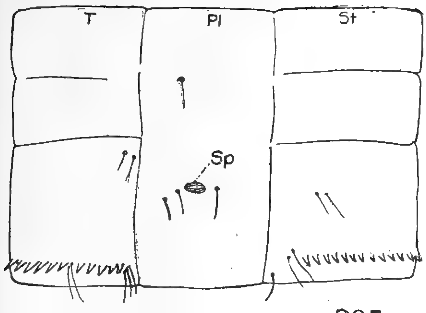


ERIOCERA LONGICORNIS, E. FULTONENSIS, AND E. SPINOSA

Eriocera longicornis, pupa: 272, male, lateral aspect; 273, male, ventral aspect; 274, female cauda, lateral aspect; 275, head of male, ventral aspect; 277, thorax of male, dorsal aspect; 278, female, lateral aspect

Eriocera fultonensis, pupa: 276, female cauda, lateral aspect; 279, female, lateral aspect

Eriocera spinosa, pupa: 280, female, lateral aspect; 281, male cauda, dorsal aspect; 282, male cauda, ventral aspect



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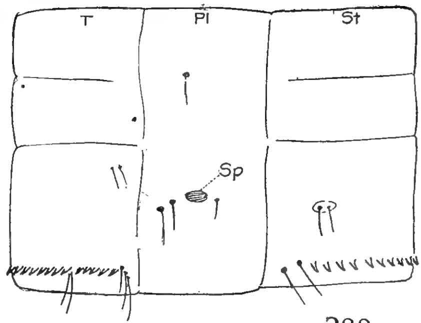

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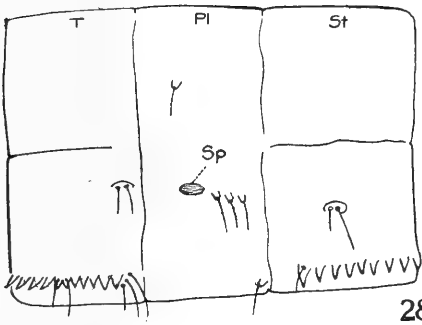

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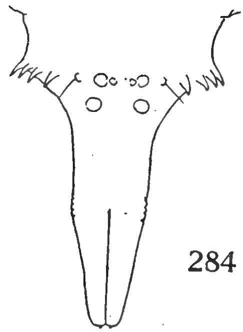
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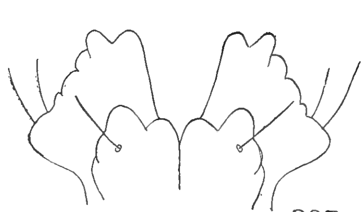
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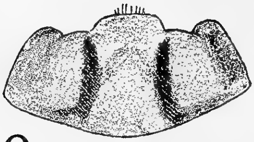
ERIOCERA SPINOSA, E. LONGICORNIS, AND E. FULTONENSIS

Eriocera spinosa, pupa: 283, fifth abdominal segment, lateral aspect (diagrammatic); 284, female cauda, dorsal aspect

Eriocera longicornis, pupa: 285, fifth abdominal segment, lateral aspect (diagrammatic); 286, male cauda, lateral aspect

Eriocera fultonensis, pupa: 287, cephalic crest of male, ventral aspect; 288, fifth abdominal segment, lateral aspect (diagrammatic)



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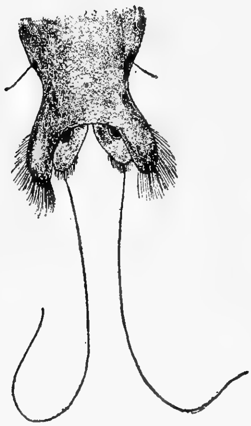

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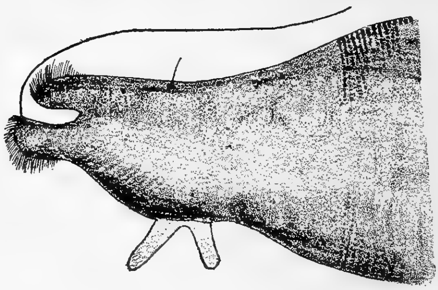
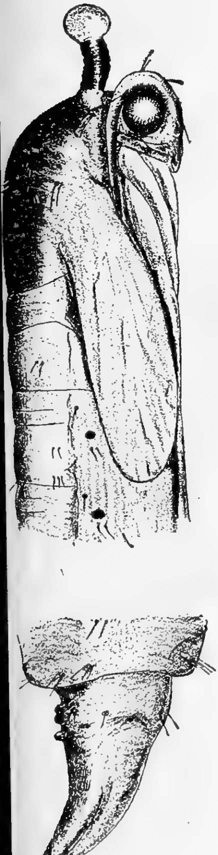


293

PENTHOPTERA ALBITARSIS

Larva: 289, labrum; 290, antenna; 291, mandible; 292, spiracular disk, dorsal aspect; 293, spiracular disk, lateral aspect

Pupa: 294, pronotal breathing horn; 295, male cauda, lateral aspect



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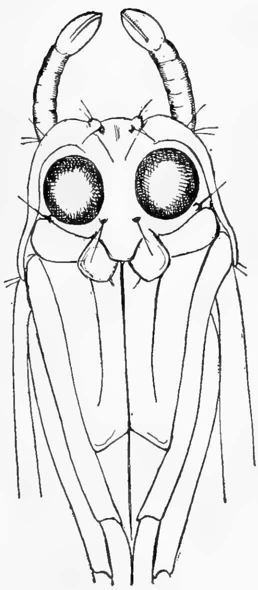

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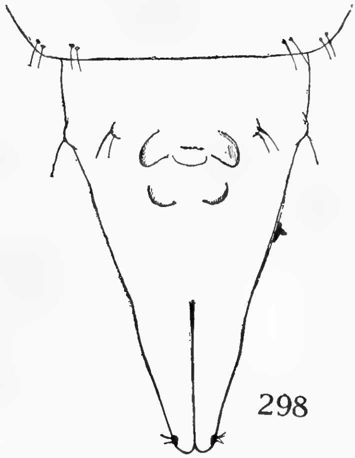

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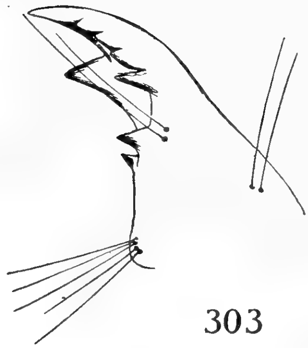
299

PENTHOPTERA ALBITARSIS, PUPA

296, Female, lateral aspect; 297, female, ventral aspect; 298, female cauda, dorsal aspect; 299, male cauda, lateral aspect

300



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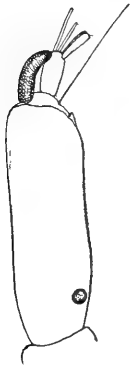

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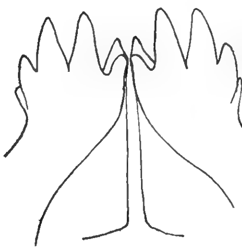

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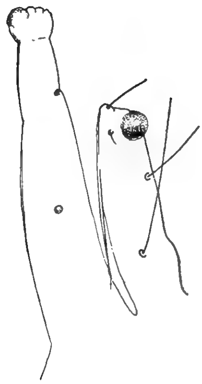

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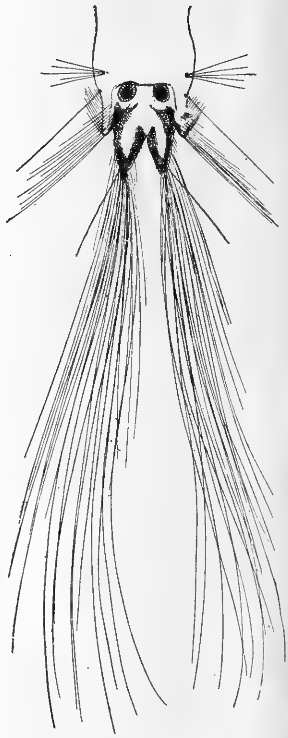
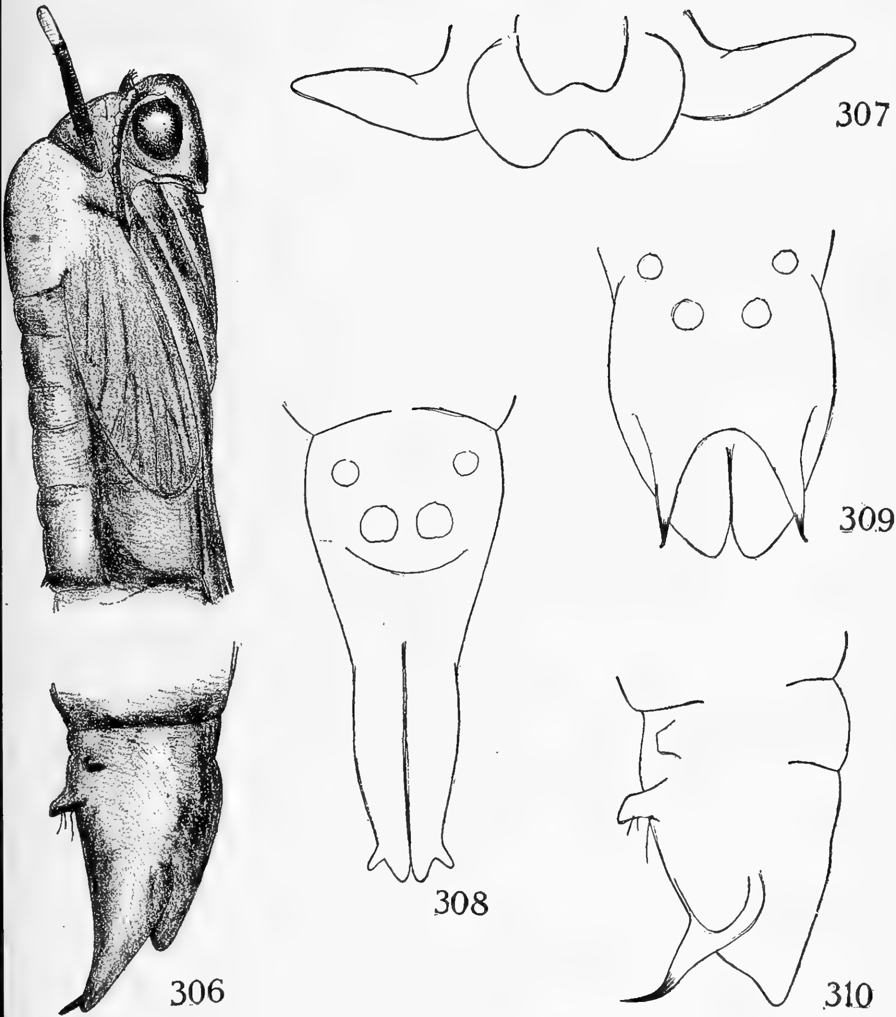


30

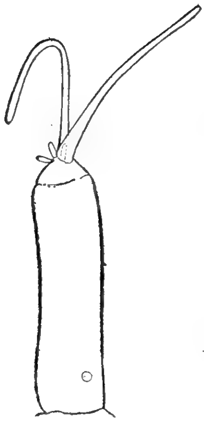
ADELPHOMYIA MINUTA (SUPPOSITION), LARVA

300, Labrum; 301, antenna; 302, mentum; 303, mandible; 304, maxilla; 305, spiracular dis



ADELPHOMYIA MINUTA (SUPPOSITION), PUPA

306, Female, lateral aspect; 307, mouth parts; 308, female cauda, dorsal aspect; 309, male cauda, dorsal aspect; 310, male cauda, lateral aspect



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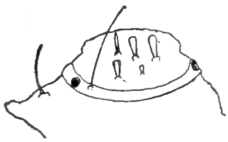

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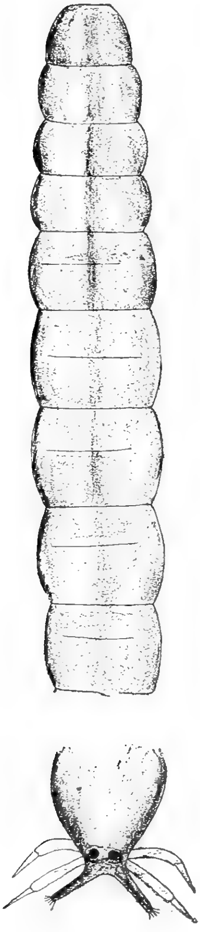

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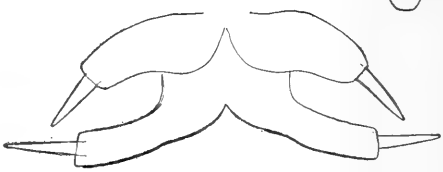
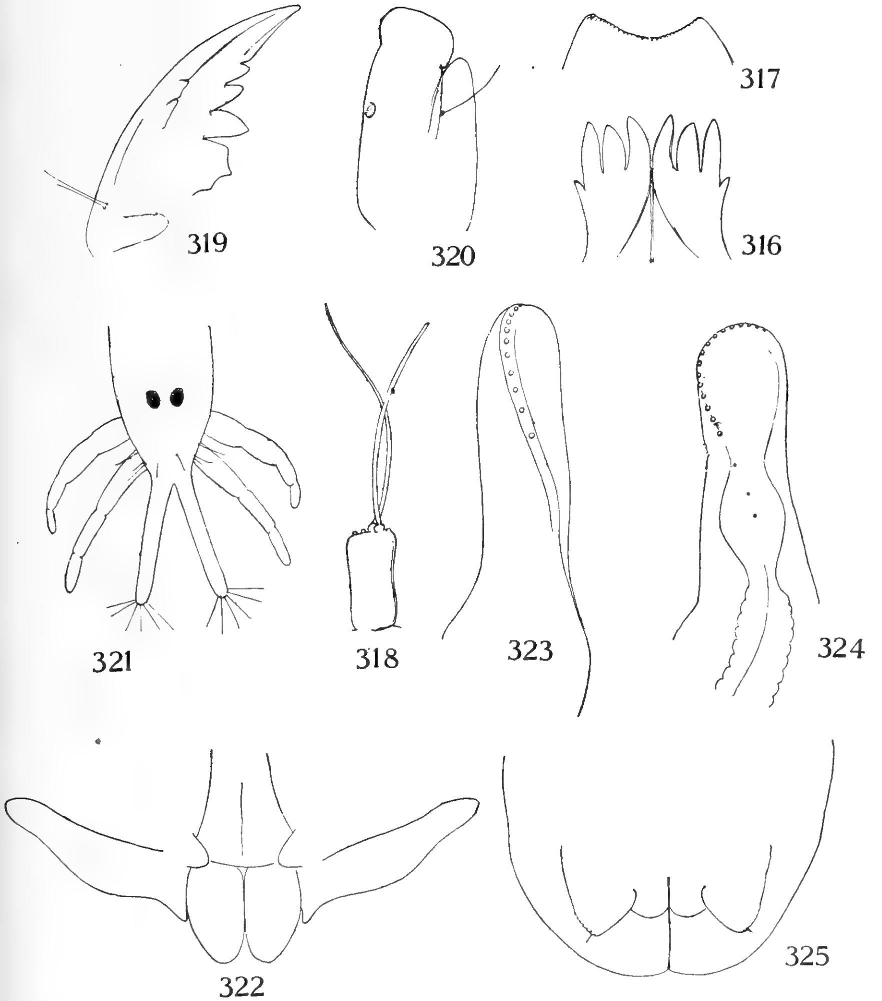


315

PEDICIA ALBIVITTA, LARVA

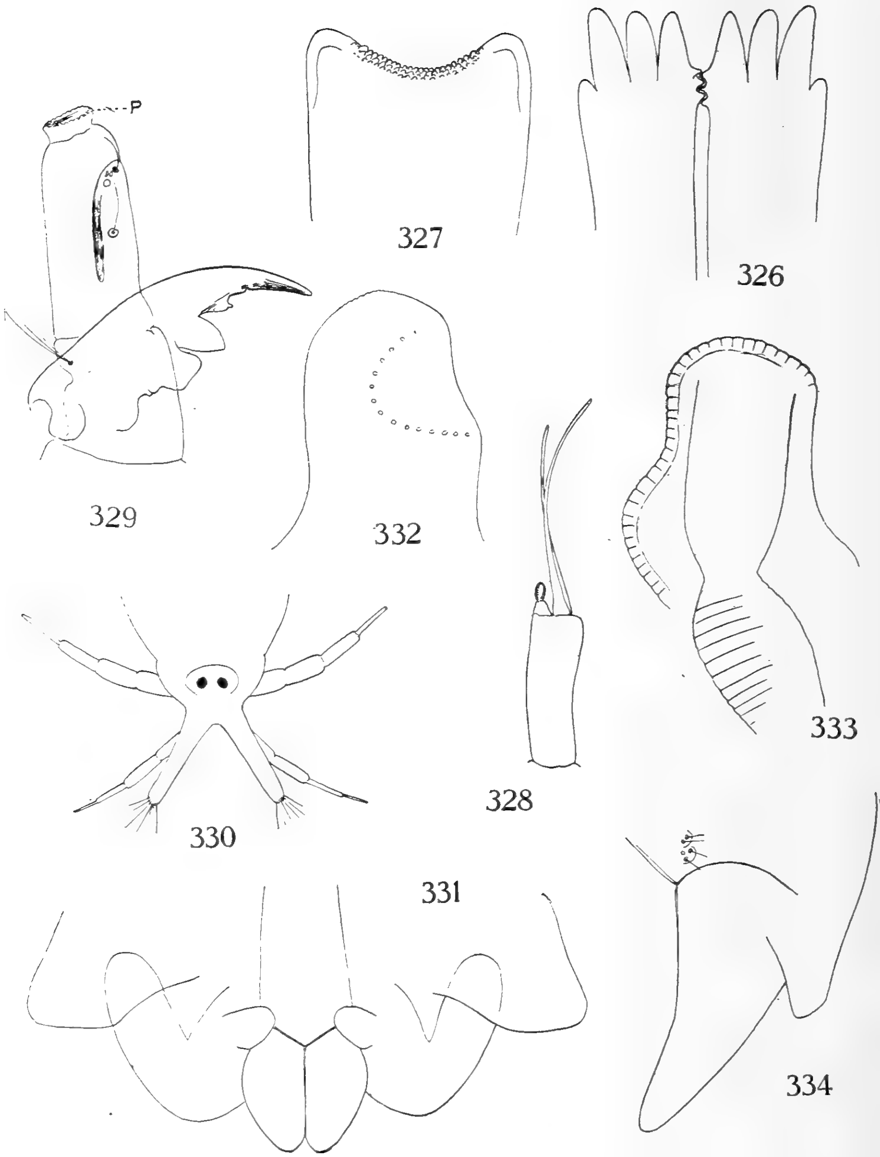
311, Dorsal aspect; 312, head capsule, ventral aspect; 313, antenna; 314, maxillary palpus; 315, anal gills, ventral aspect



RHAPHIDOLABINA FLAVEOLA

Larva: 316, mentum; 317, hypopharynx; 318, antenna; 319, mandible; 320, maxilla; 321, spiracular disk

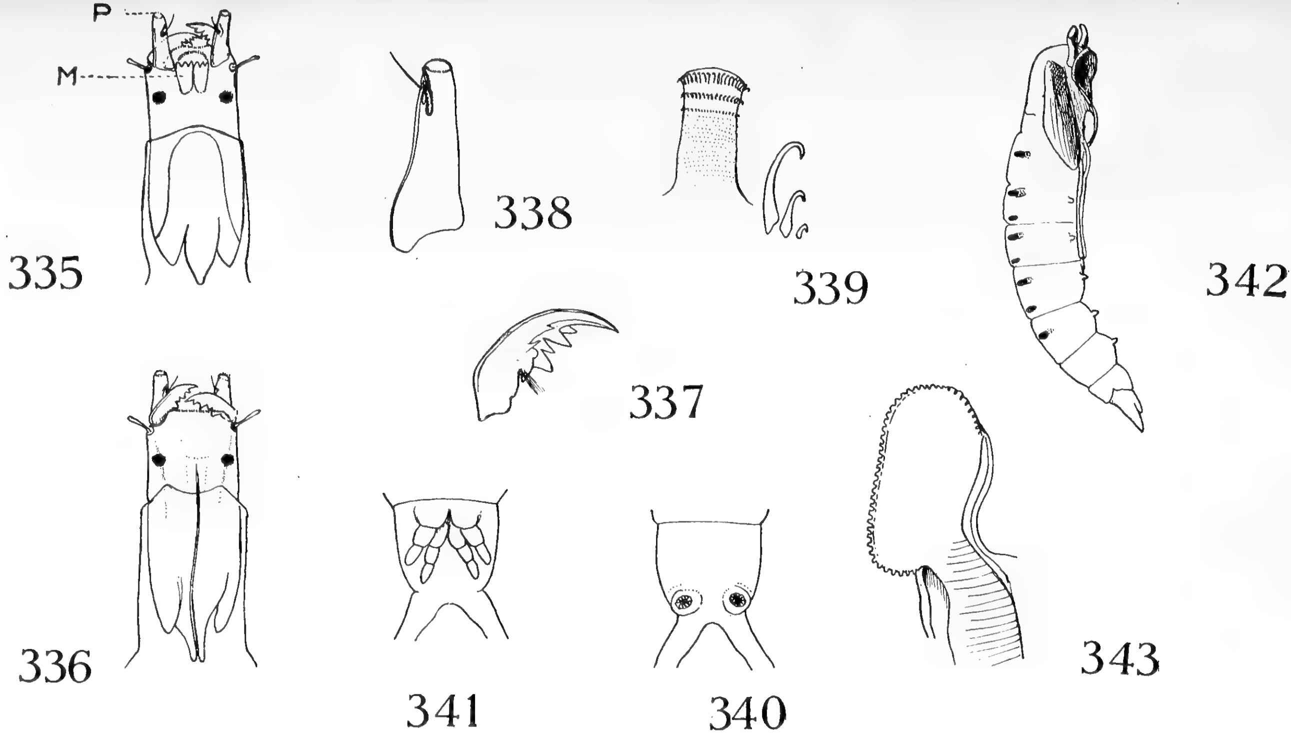
Pupa: 322, mouth parts; 323, pronotal breathing horn, dorsal aspect; 324, pronotal breathing horn, lateral aspect; 325, male cauda, dorsal aspect



TRICYPHONA INCONSTANS

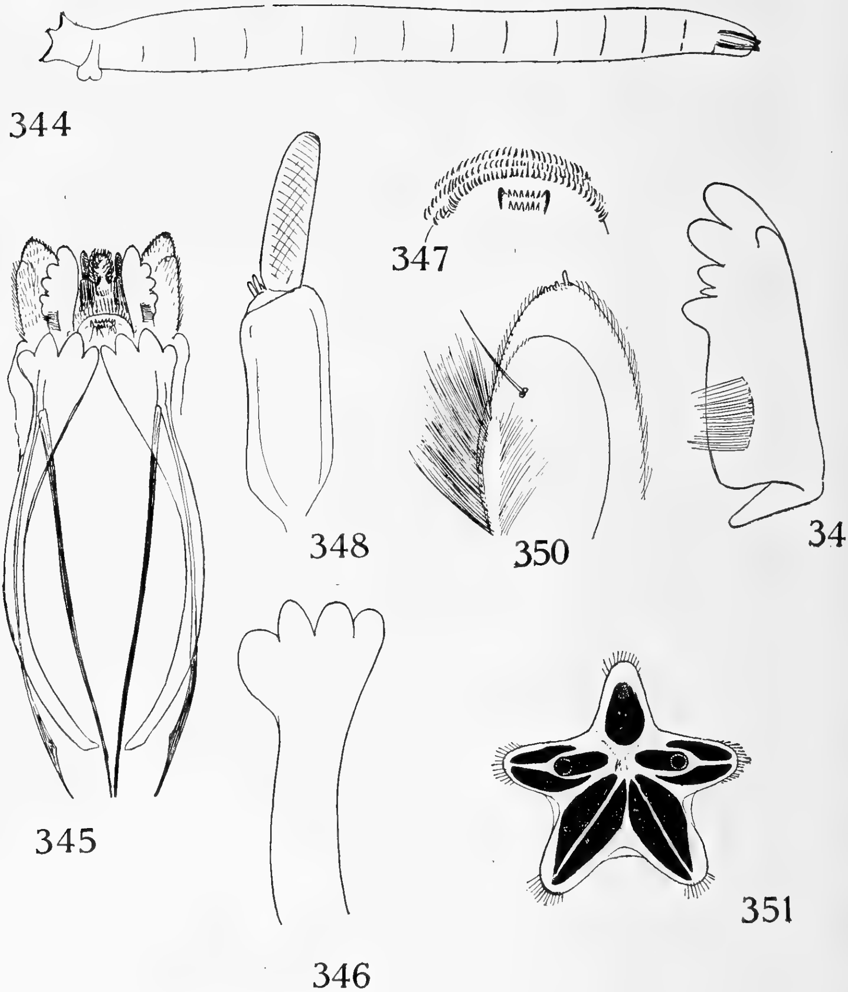
Larva: 326, mentum; 327, hypopharynx; 328, antenna; 329, mandible and maxilla; 330, spiracular disk

Pupa: 331, mouth parts; 332, pronotal breathing horn, dorsal aspect; 333, pronotal breathing horn, lateral aspect; 334, female cauda, lateral aspect



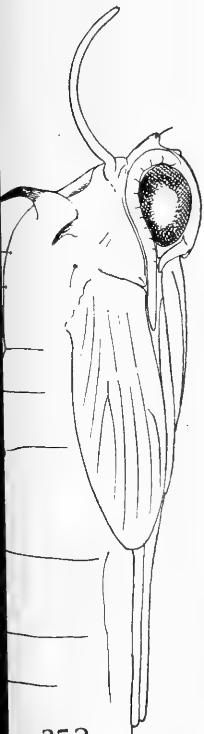
DICRANOTA BIMACULATA (AFTER MIALL)

Larva: 335, head capsule, ventral aspect; 336, head capsule, dorsal aspect; 337, mandible; 338, maxillary palpus; 339, abdominal pseudopods; 340, spiracular disk, dorsal aspect; 341, anal gills
Pupa: 342, female, lateral aspect; 343, pronotal breathing horn



MOLOPHILUS HIRTIPENNIS, LARVA

344, Lateral aspect; 345, head capsule, ventral aspect; 346, mental plate; 347, hypopharynx; 348, antenna; 349, mandible; 350, maxilla; 351, spiracular disk



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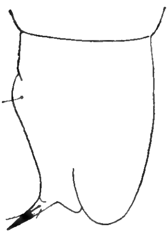

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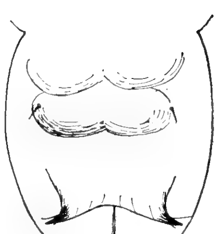

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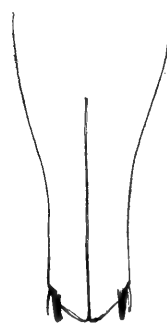

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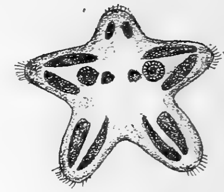
MOLOPHILUS HIRTIPENNIS, PUPA

52, Female, lateral aspect; 353, male cauda, lateral aspect; 354, male cauda, dorsal aspect; 355, female cauda, lateral aspect; 356, female cauda, dorsal aspect



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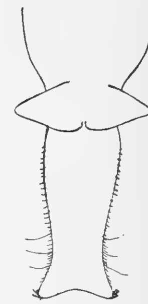

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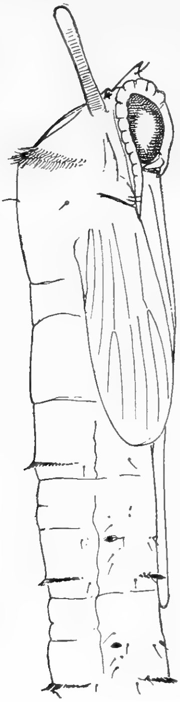

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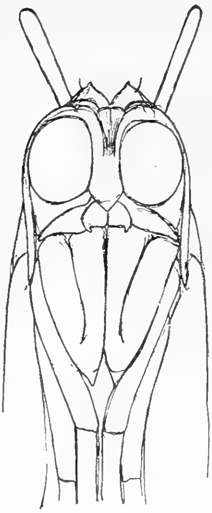

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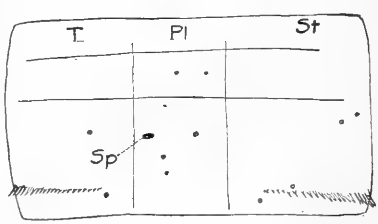

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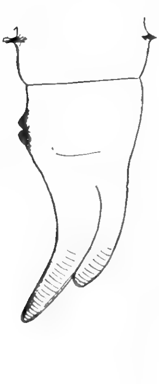

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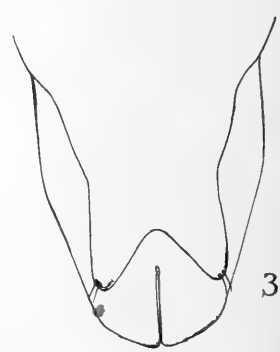

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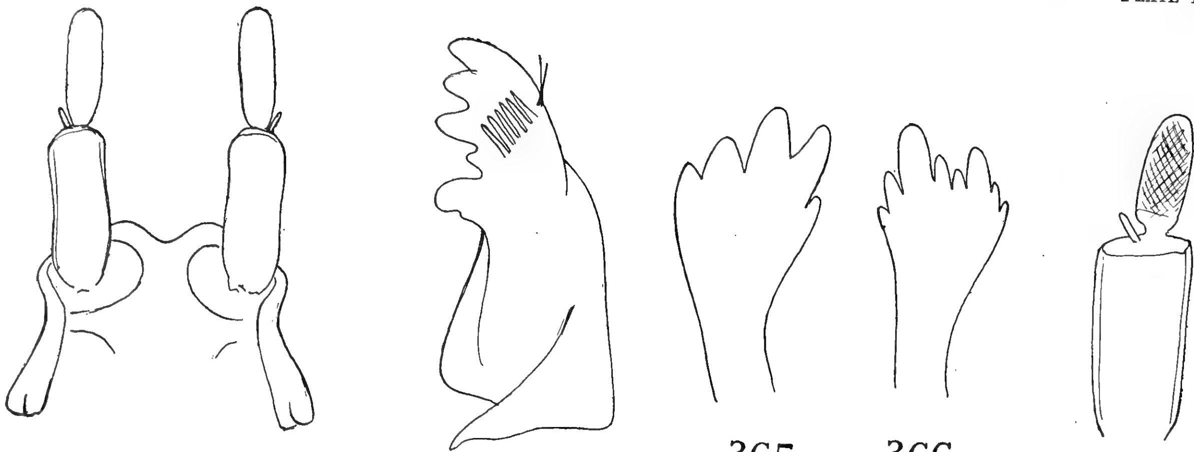
ERIOPTERA MEGOPHTHALMA

Larva: 357, spiracular disk; 358, anal gills, ventral aspect
Pupa: 359, female, lateral aspect; 360, female, ventral aspect; 361, fifth abdominal se ment, lateral aspect (diagrammatic); 362, male cauda, lateral aspect; 363, male cauda, dors aspect

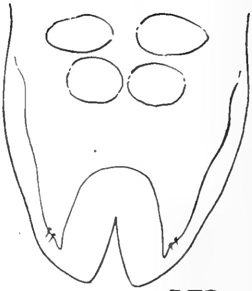


364 368 365 366 367

ERIOPTERA CHLOROPHYLLA, LARVA

364, Head capsule, showing bases of antennae; 365, mental bar; 366, aberration of mental bar; 367, antenna; 368, mandible

371



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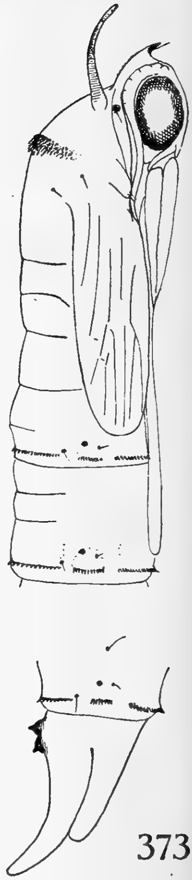

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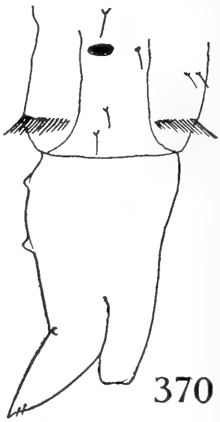
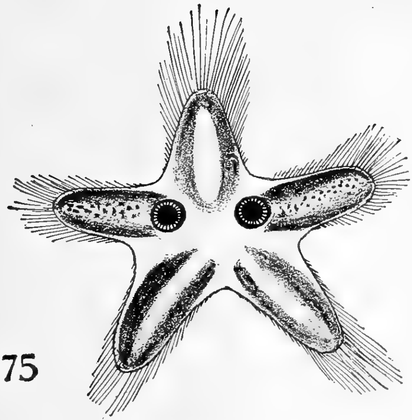


370

ERIOPTERA CHLOROPHYLLA, E. SEPTEMTRIONIS, AND E. ARMATA

Erioptera chlorophylla, pupa: 369, female, lateral aspect; 370, female cauda, lateral aspect
Erioptera septemtrionis, pupa: 371, male cauda, lateral aspect; 372, male cauda, dorsal aspect
Erioptera armata, pupa: 373, female, lateral aspect



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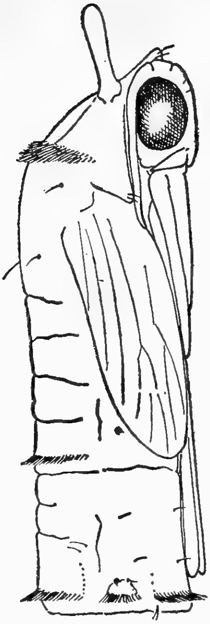

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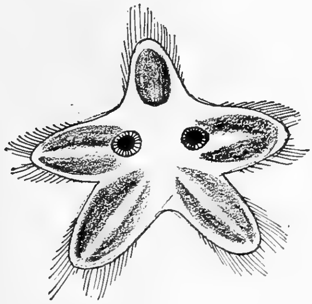

379

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378

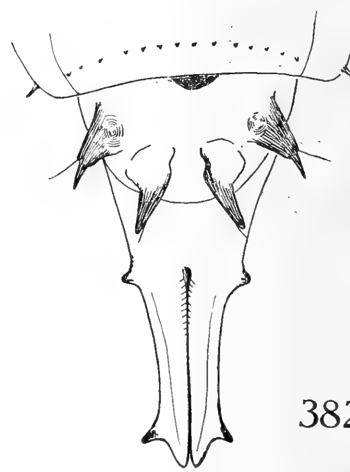
ORMOSIA NUBILA, O. INNOCENS, AND O. MEIGENII

Ormosia nubila, larva: 374, mandible; 375, spiracular disk

Ormosia innocens, pupa: 376, female, lateral aspect; 377, male cauda, dorsal aspect; 378, male cauda, lateral aspect

Ormosia meigenii, larva: 379, spiracular disk

381



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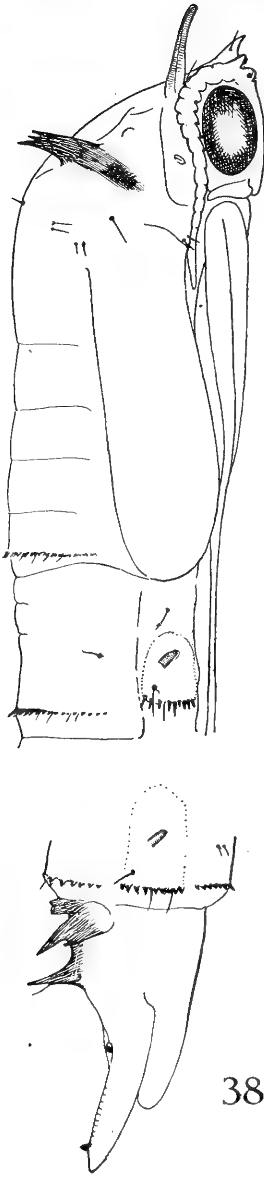
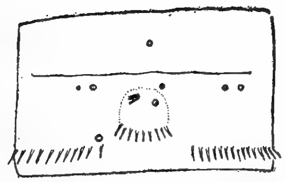


380

ORMOSIA NUBILA, PUPA

380, Female, lateral aspect; 381, cephalic crest of female, ventral aspect; 382, female cauda, dorsal aspect

383



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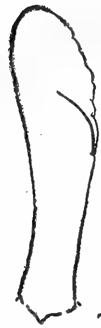

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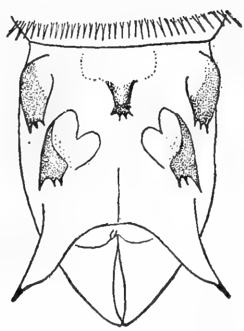

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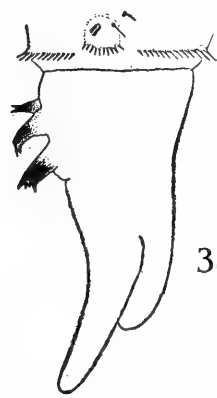
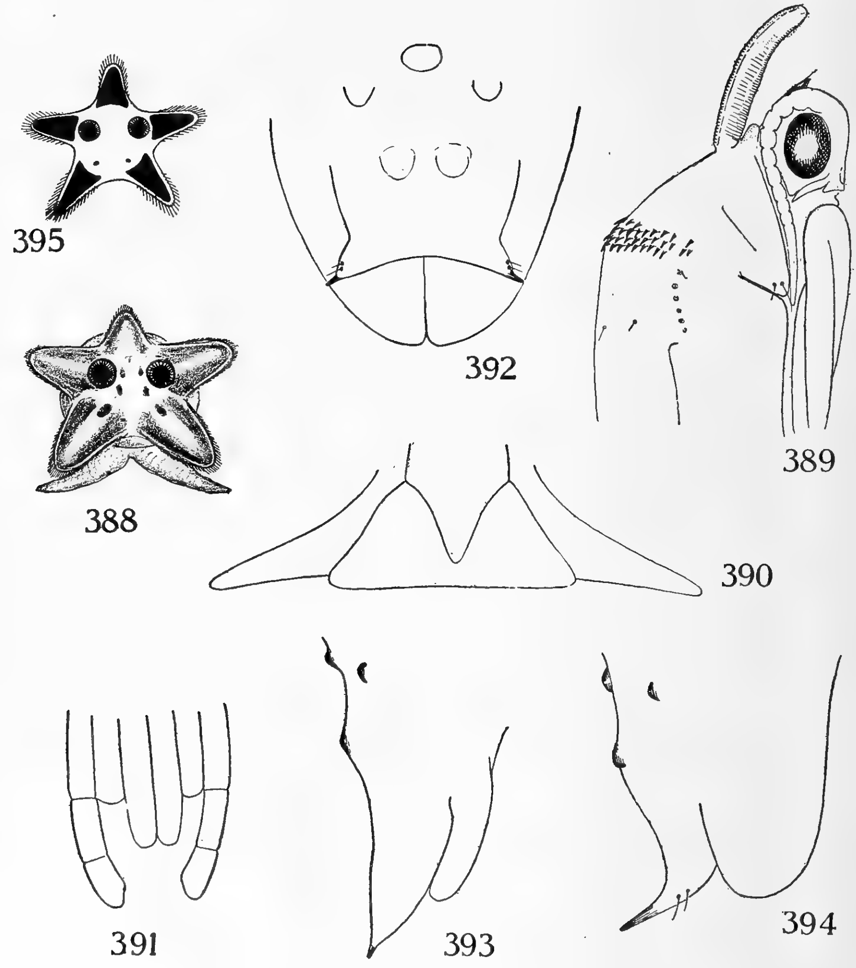


387

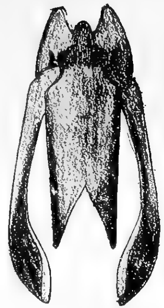
ORMOSIA NIGRIPILA, PUPA

383, Male, lateral aspect; 384, pronotal breathing horn; 385, fifth abdominal segment, lateral aspect (diagrammatic); 386, male cauda, dorsal aspect; 387, female cauda, lateral aspect



HELOBIA HYBRIDA AND TRIMICRA PILIPES

Helobia hybrida, larva: 388, spiracular disk
Helobia hybrida, pupa: 389, female, lateral aspect; 390, mouth parts; 391, arrangemen of leg sheaths; 392, male cauda, dorsal aspect; 393, female cauda, lateral aspect; 394, mal cauda, lateral aspect
Trimicra pilipes, larva: 395, spiracular disk (after Gerbig)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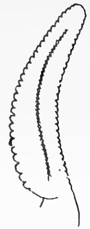
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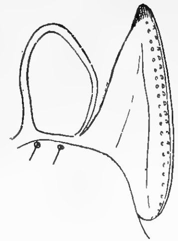
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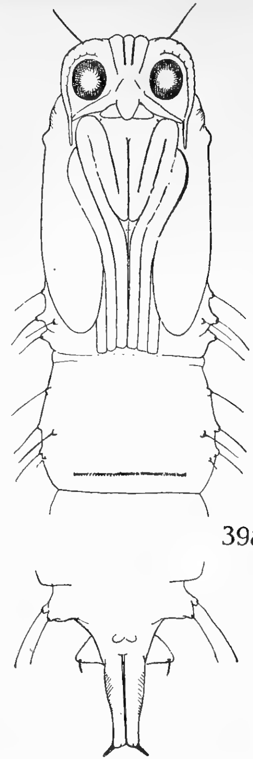
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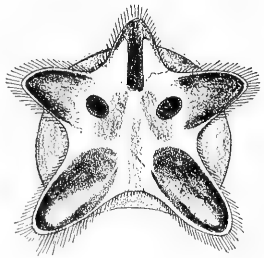
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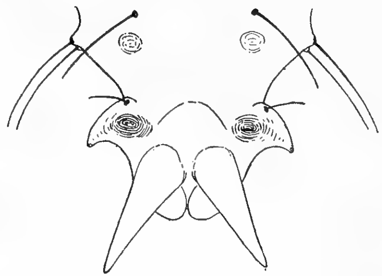
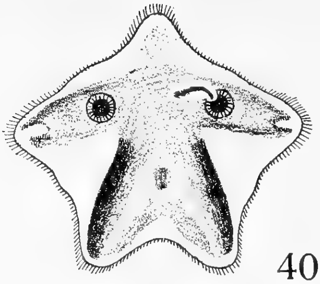

401

GNOPHOMYIA TRISTISSIMA

Larva: 396, head capsule (after Malloch); 397, spiracular disk (after Malloch)
Pupa: 398, female, ventral aspect; 399, pronotal breathing horn, lateral aspect; 400, pronotal breathing horn and thoracic crest, dorsal aspect; 401, male cauda, dorsal aspect



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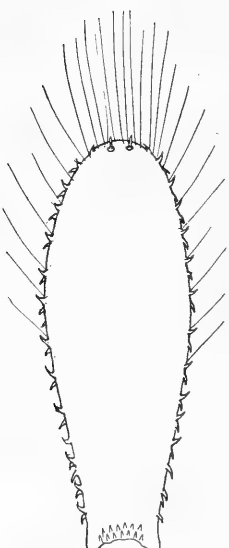
402

404



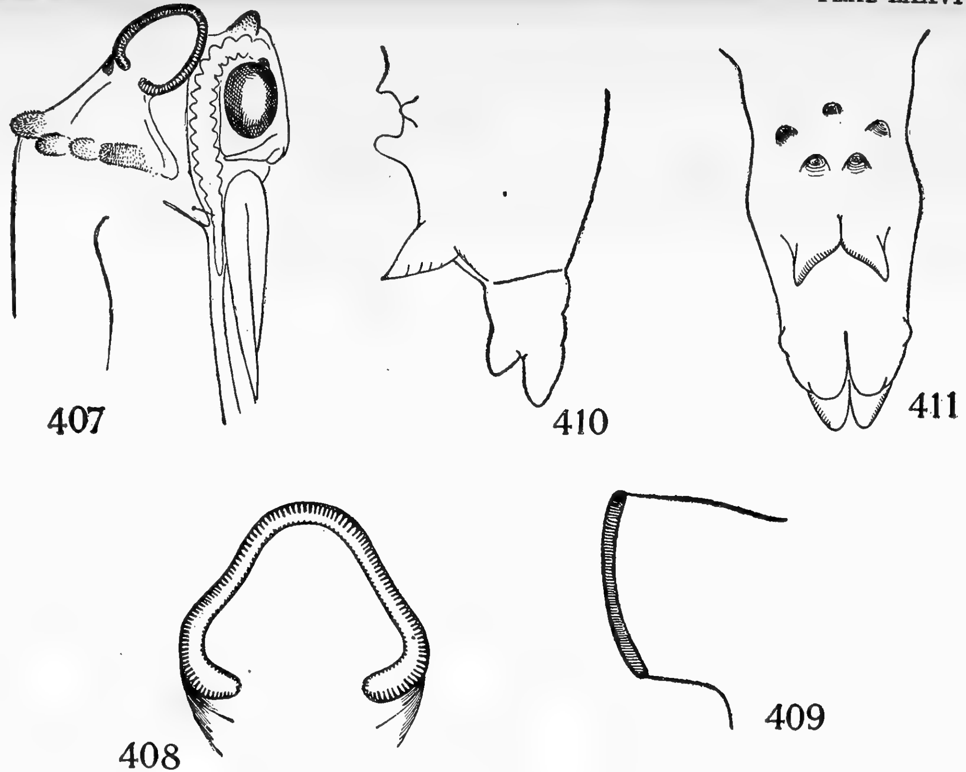
406

405

GONOMYIA ALEXANDERI AND ERIOPTERINE NO. 1

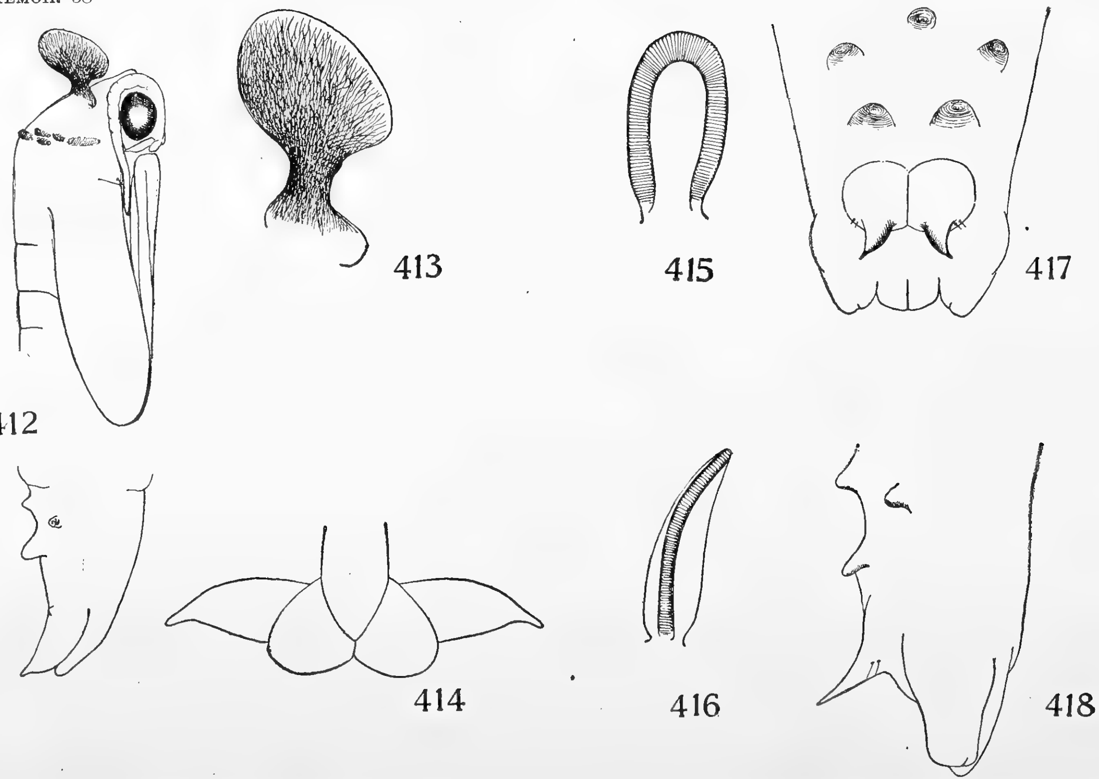
Gonomyia alexanderi, larva: 402, mandible; 403, spiracular disk

Eriopterine No. 1, larva: 404, lateral aspect; 405, spiracular disk and anal gills; 406, lobe of spiracular disk, enlarged



GONOMYIA ALEXANDERI, PUPA

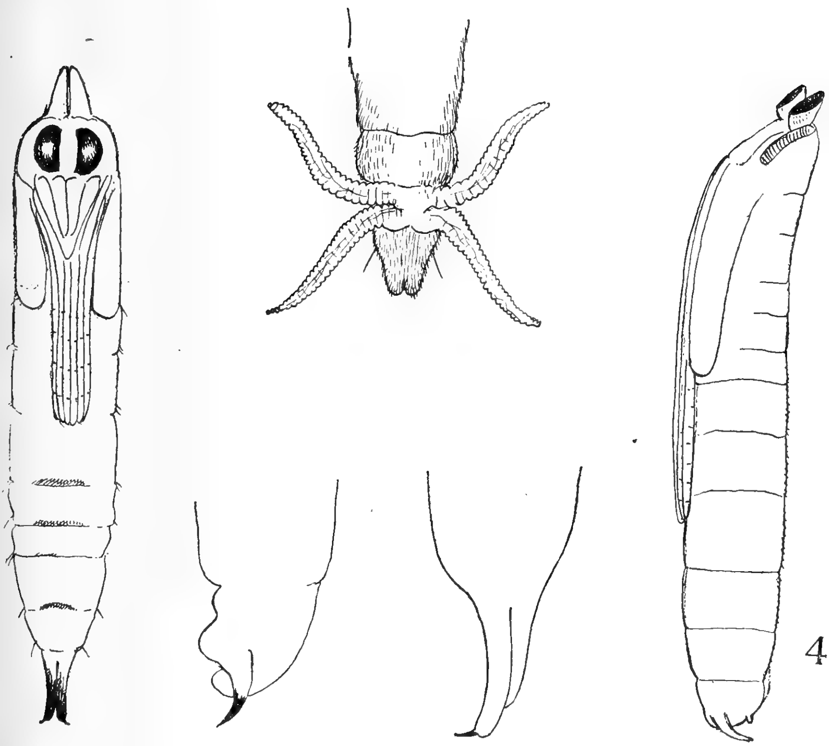
407, Male, lateral aspect; 408, pronotal breathing horn; 409, pronotal breathing horn, lateral aspect; 410, male cauda, lateral aspect; 411, male cauda, dorsal aspect



GONOMYIA SULPHURELLA AND G. KANSENSIS

Gonomyia sulphurella, pupa: 412, female, lateral aspect; 413, pronotal breathing horn, lateral aspect; 414, mouth parts
Gonomyia kansensis, pupa: 415, pronotal breathing horn, lateral aspect; 416, pronotal breathing horn, ventral aspect;
417, male cauda, dorsal aspect; 418, male cauda, lateral aspect

420

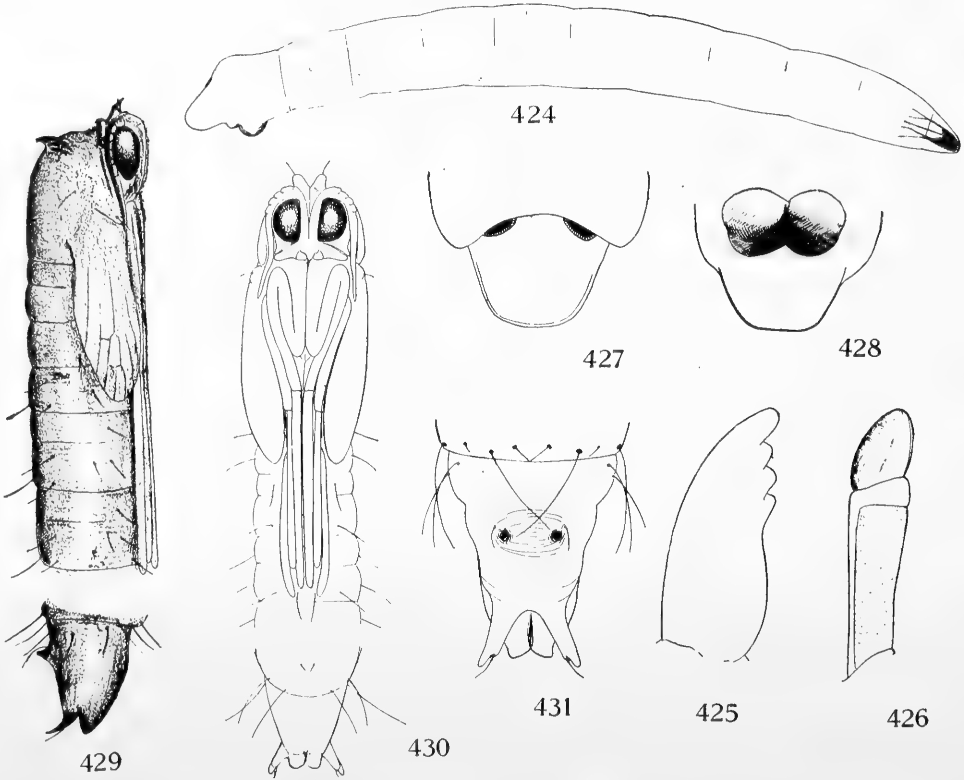


419

421 422 423

TRENTEPOHLIA PENNIPES AND T. BROMELIADICOLA

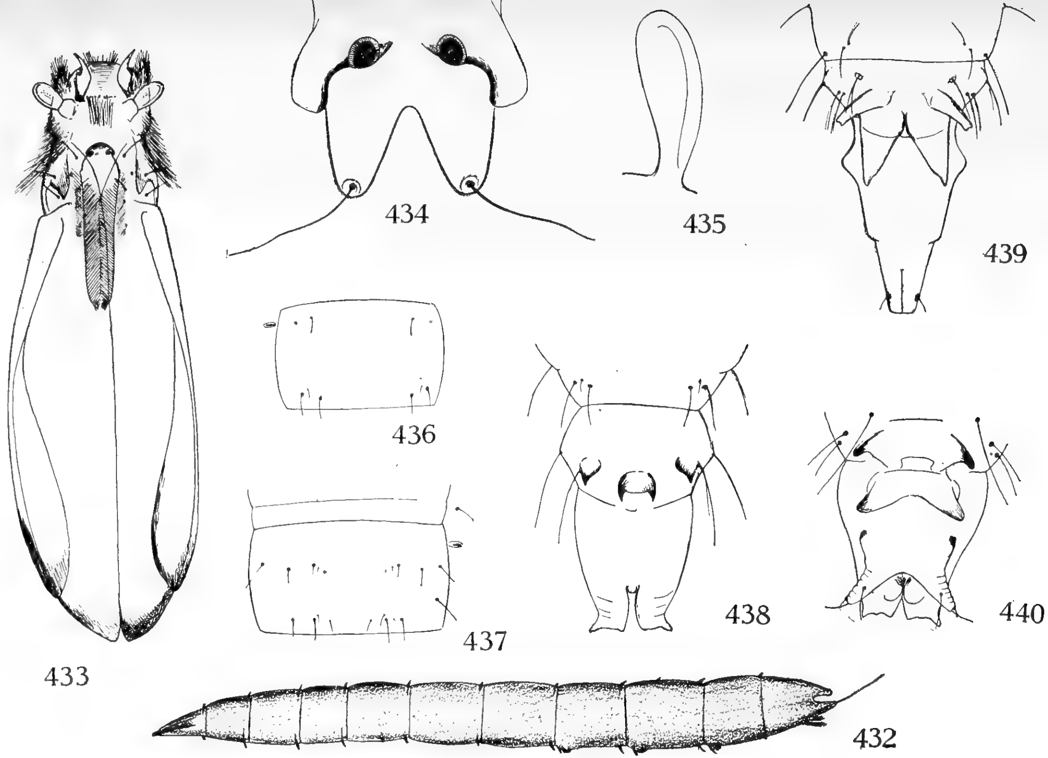
Trentepohlia pennipes, pupa: 419, lateral aspect (after De Meijere)
Trentepohlia bromeliadicola, larva (after Picado): 420, anal gills
Trentepohlia bromeliadicola, pupa (after Picado): 421, female, ventral aspect; 422, male cauda, lateral aspect; 423, female cauda, lateral aspect



TEUCHOLABIS COMPLEXA

Larva: 424, lateral aspect; 425, mandible; 426, antenna; 427, spiracular disk, dorsal aspect; 428, anal gills

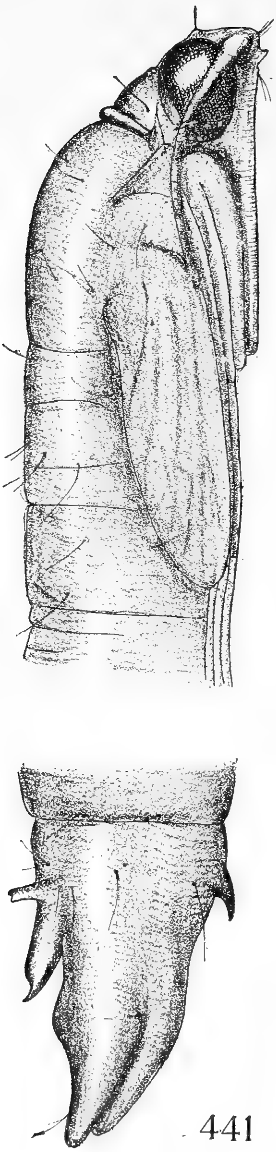
Pupa: 429, male, lateral aspect; 430, male, ventral aspect; 431, male cauda, dorsal aspect



ELEPHANTOMYIA WESTWOODI

Larva: 432, lateral aspect; 433, head capsule, ventral aspect; 434, spiracular disk, dorsal aspect

Pupa: 435, pronotal breathing horn; 436, fifth abdominal segment, ventral aspect (diagrammatic); 437, fifth abdominal segment, dorsal aspect; 438, male cauda, ventral aspect; 439, female cauda, dorsal aspect; 440, male cauda, dorsal aspect



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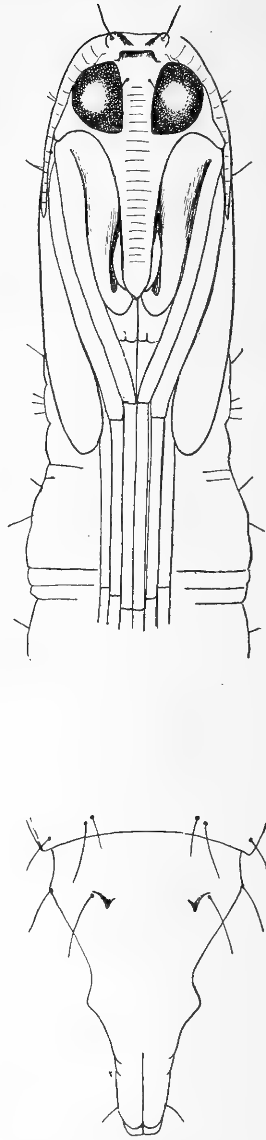
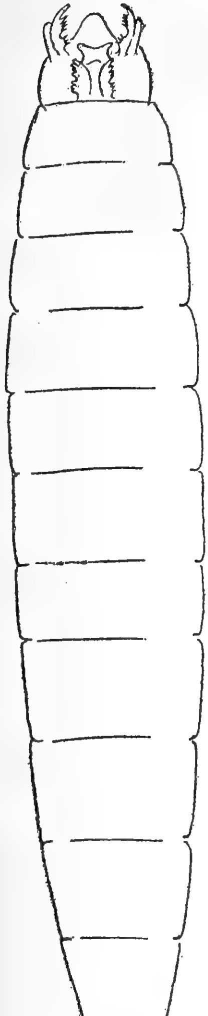
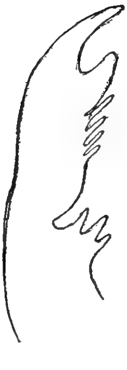


442

ELEPHANTOMYIA WESTWOODI, PUPA

441, Female, lateral aspect; 442, female, ventral aspect





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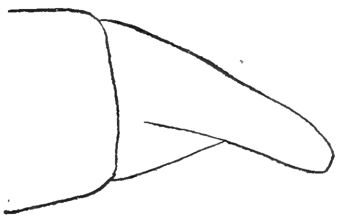

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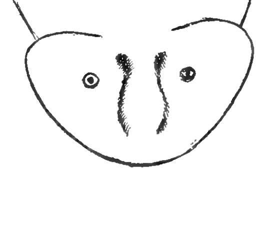
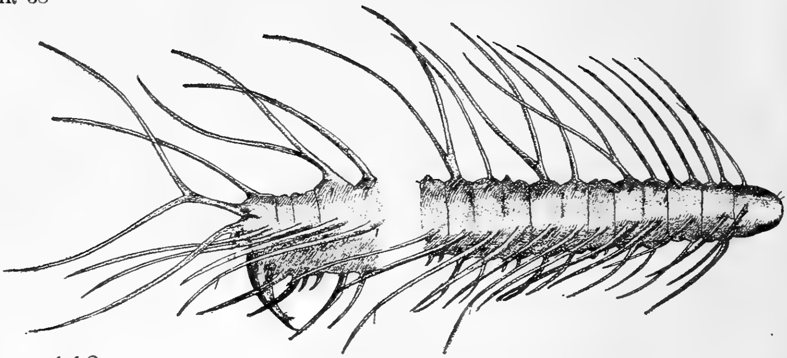


447

443

CHIONEA ARANEOIDES, LARVA (AFTER BRAUER)

443, Dorsal aspect; 444, mandible; 445, possibly mental plate; 446, spiracular disk, lateral aspect; 447, spiracular disk, dorsal aspect



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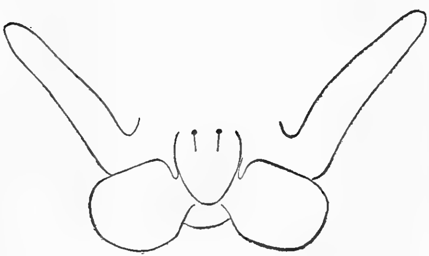

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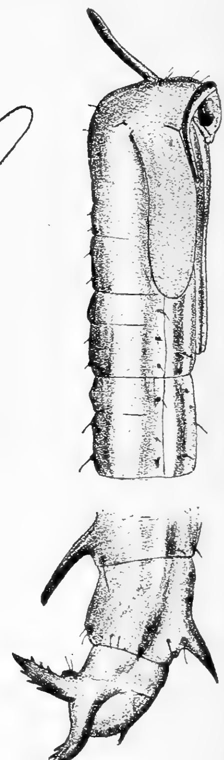

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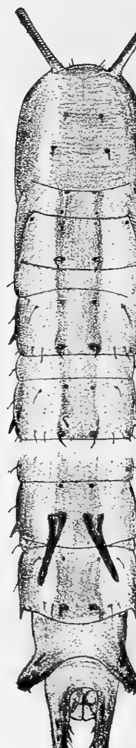
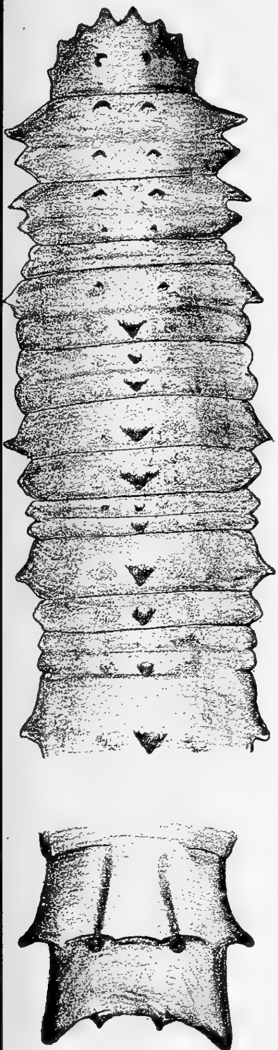


450

PHALACROCERA REPLICATA AND TRIOGMA TRISULCATA

Phalacrocera replicata, larva: 448, lateral aspect
Phalacrocera replicata, pupa: 449, male, lateral aspect; 450, male, dorsal aspect; 451, mouth parts
Triogma trisulcata: 452, larva (after Steinmann)



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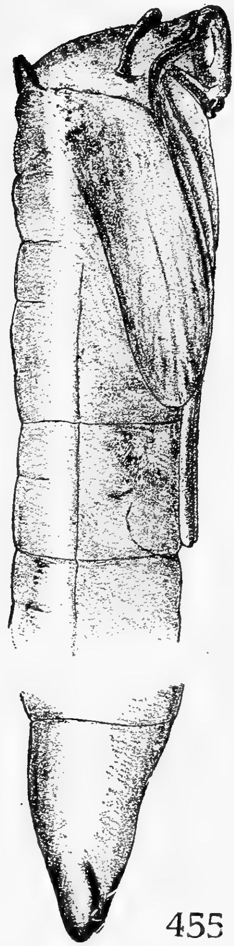

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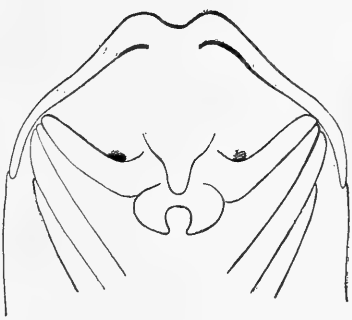
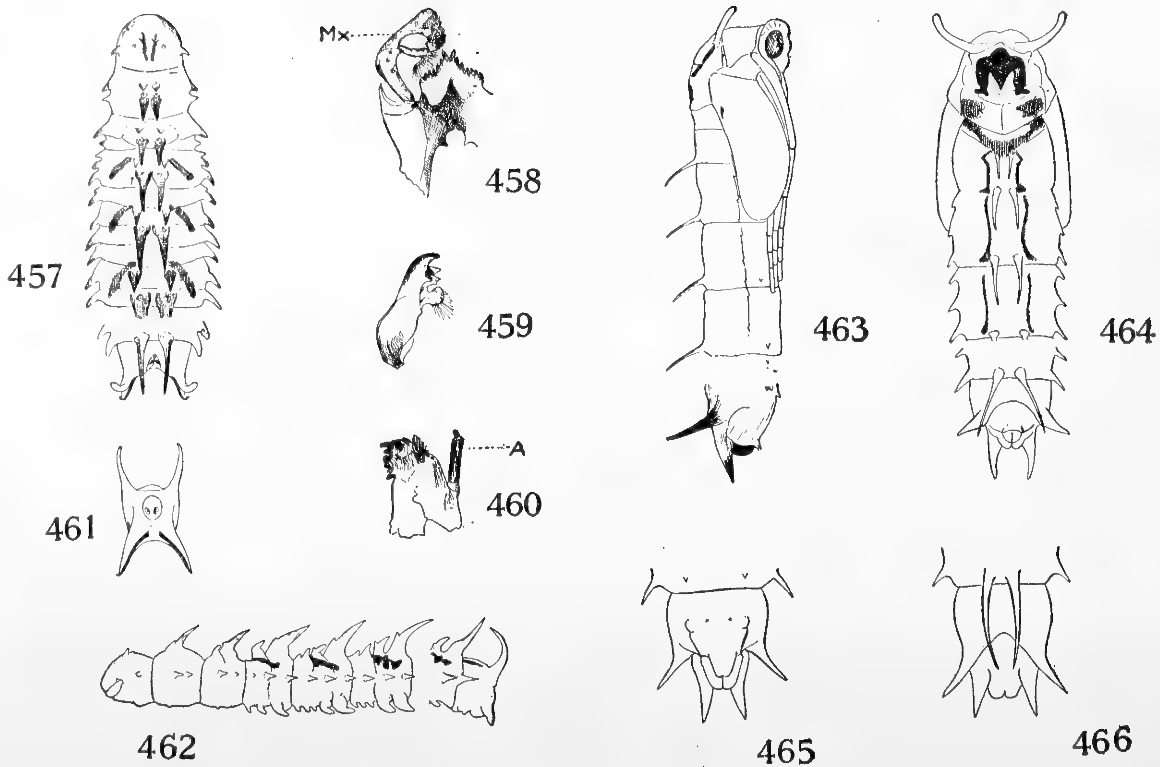


453

456

CYLINDROTOMA SPLENDENS

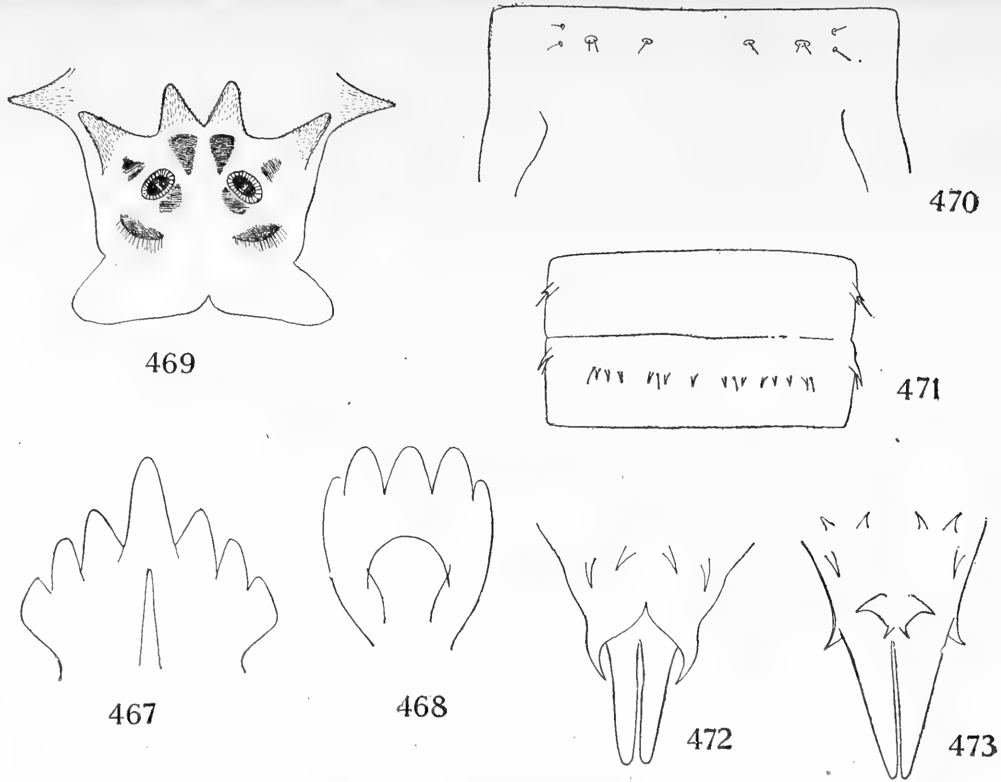
Larva: 453, dorsal aspect; 454, mandible
Pupa: 455, female, lateral aspect; 456, head of female, ventral aspect



LIOGMA NODICORNIS

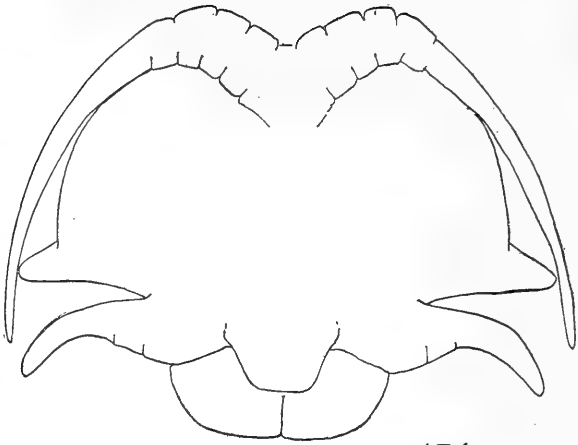
Larva: 457, dorsal aspect; 458, mentum and maxilla; 459, mandible; 460, mandible and antenna; 461, spiracular disk; 462, lateral aspect of larva

Pupa: 463, male, lateral aspect; 464, male, dorsal aspect; 465, female cauda, ventral aspect; 466, female cauda, dorsal aspect



OROPEZA OBSCURA

Larva: 467, mentum; 468, hypopharynx; 469, spiracular disk
Pupa: 470, metanotum (diagrammatic); 471, fifth abdominal tergite (diagrammatic); 472, female cauda, dorsal aspect; 473, female cauda, ventral aspect



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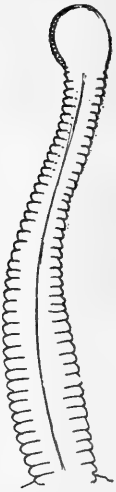

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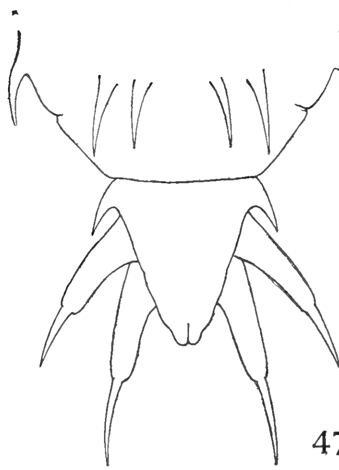

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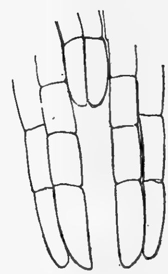
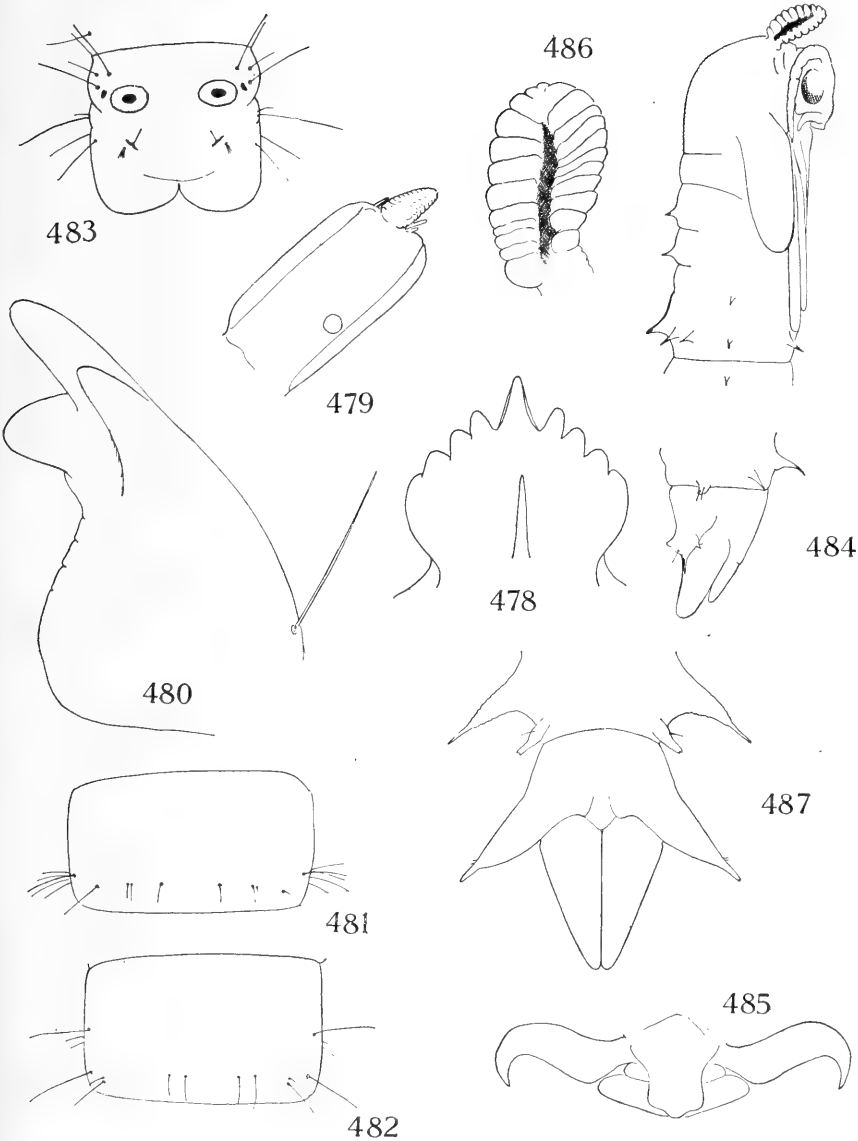


476

BRACHYPREMNA DISPELLENS, PUPA

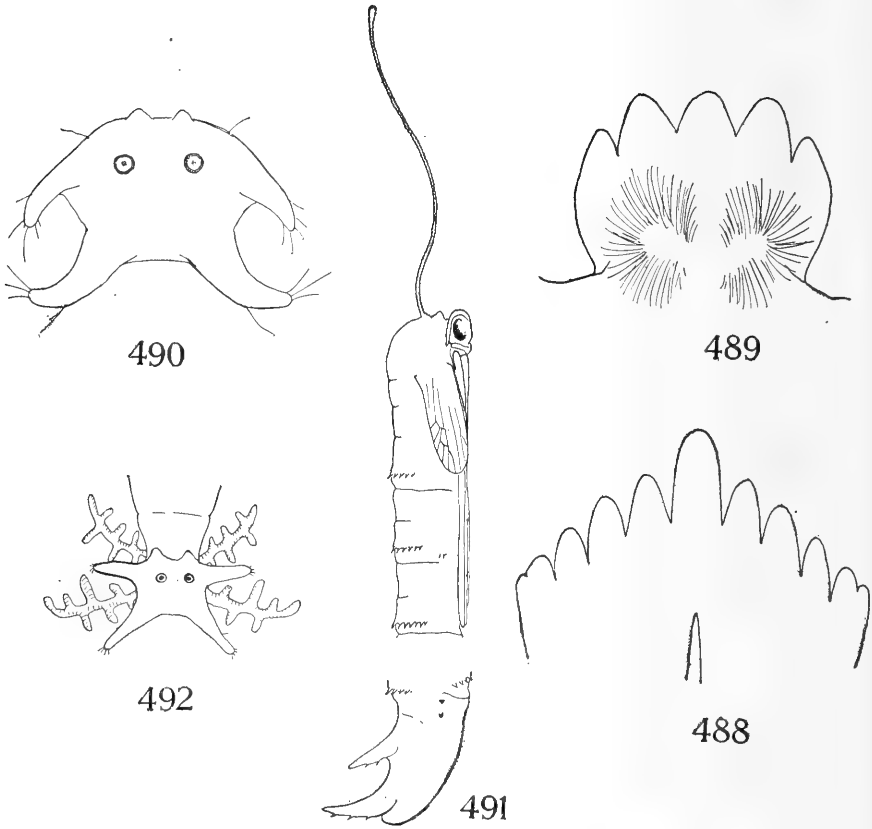
474, Head, ventral aspect; 475, pronotal breathing horn; 476, arrangement of leg sheaths; 477, male cauda, ventral aspect



TANYPTERA FRONTALIS

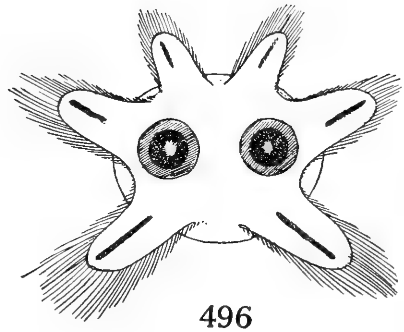
Larva: 478, mentum; 479, antenna; 480, mandible; 481, fifth abdominal segment, dorsal aspect (diagrammatic); 482, fifth abdominal segment, ventral aspect (diagrammatic); 483, spiracular disk

Pupa: 484, female, lateral aspect; 485, mouth parts; 486, pronotal breathing horn; 487, female cauda, dorsal aspect



LONGURIO TESTACEUS AND AESHNASOMA RIVERTONENSIS

Longurio testaceus, larva: 488, mentum; 489, hypopharynx; 490, spiracular disk
Longurio testaceus, pupa: 491, male, lateral aspect
Aeshnasoma rivertonensis, larva: 492, spiracular disk, showing branched anal gills (after Johnson)



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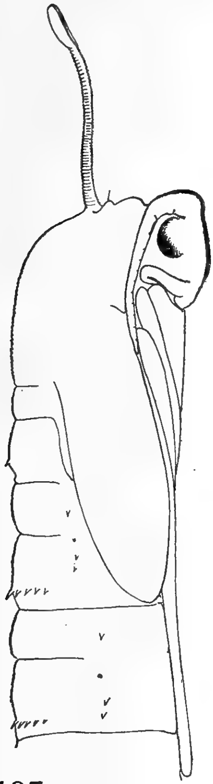

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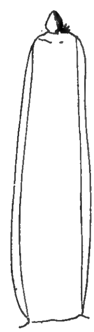

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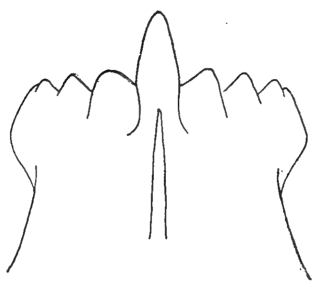

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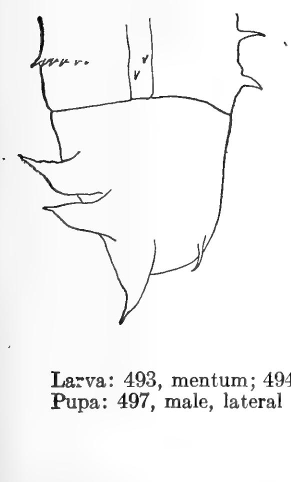
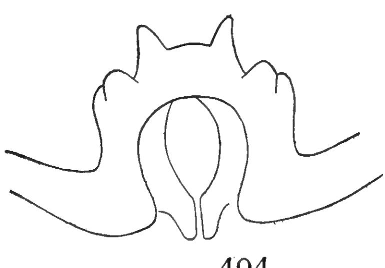
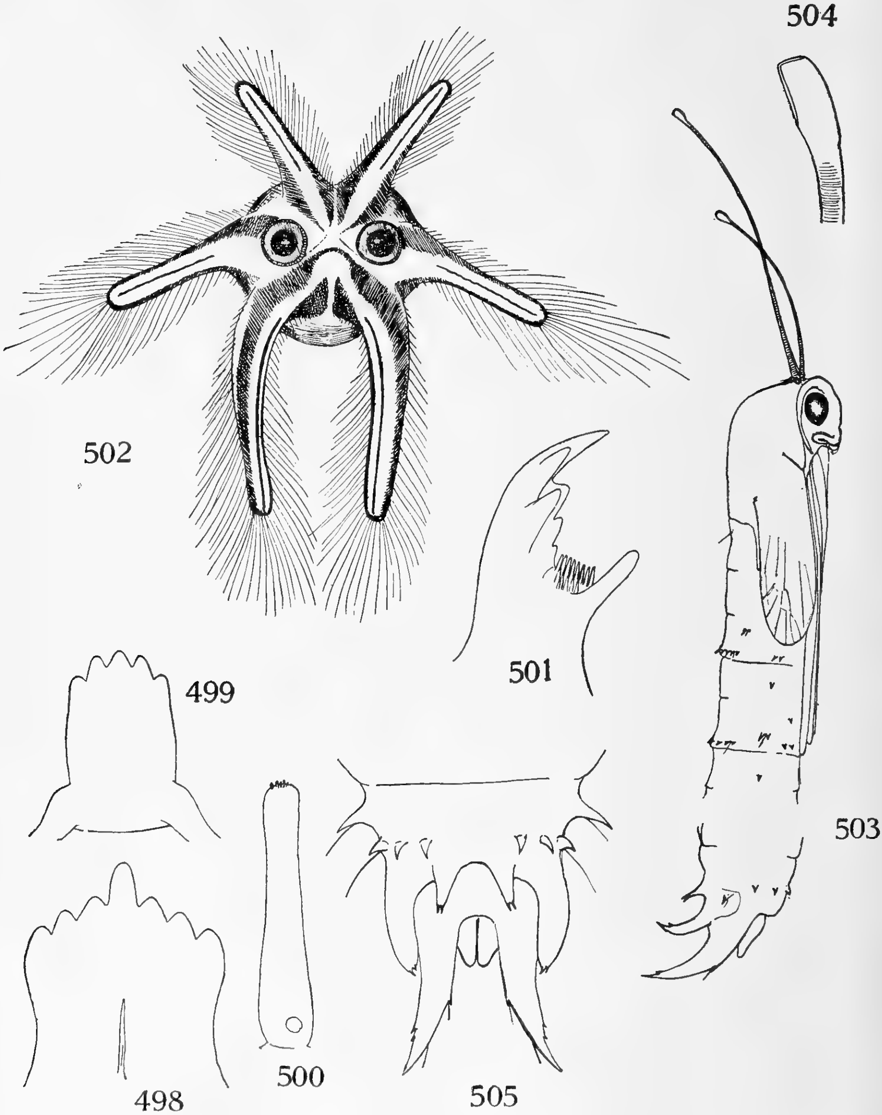




494

HOLORUSIA RUBIGINOSA

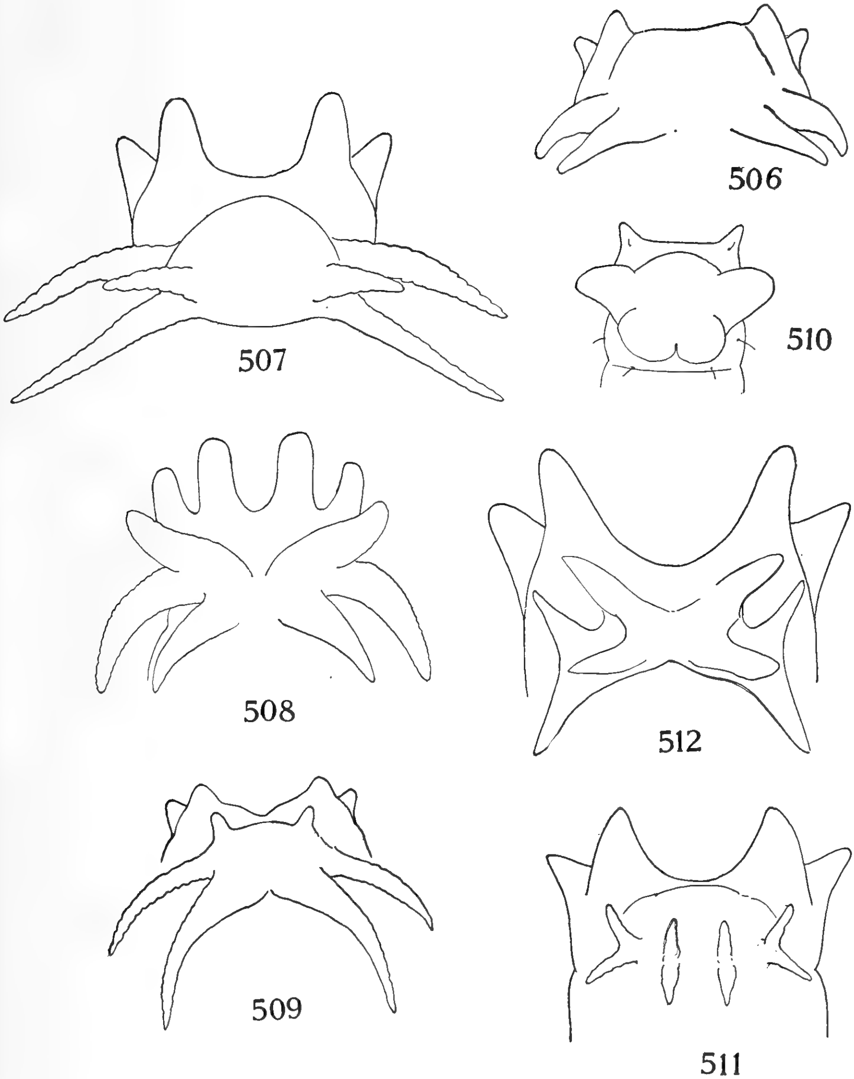
Larva: 493, mentum; 494, hypopharynx; 495, antenna; 496, spiracular disk
Pupa: 497, male, lateral aspect



PRIONOCERA FUSCIPENNIS

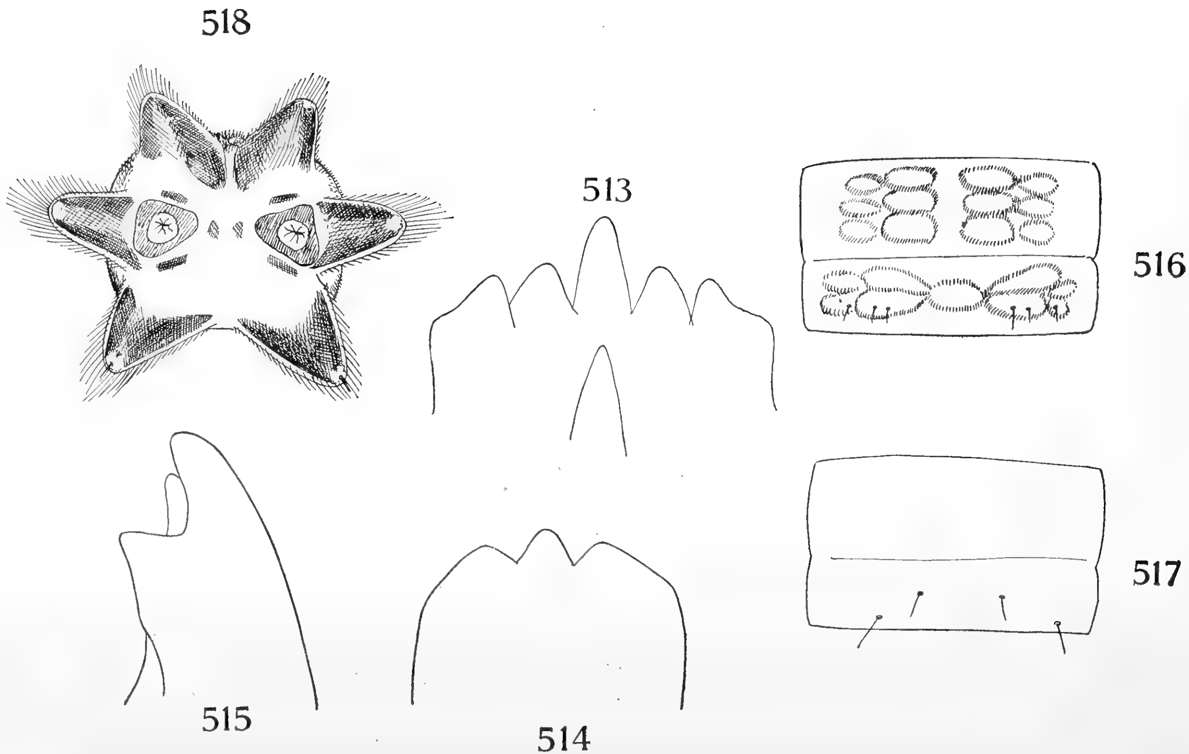
Larva: 498, mentum; 499, hypopharynx; 500, antenna; 501, mandible; 502, spiracular disk

Pupa: 503, lateral aspect; 504, tip of pronotal breathing horn; 505, male cauda, dorsal aspect



TYPES OF ANAL GILLS IN GENUS TIPULA, VENTRAL ASPECT

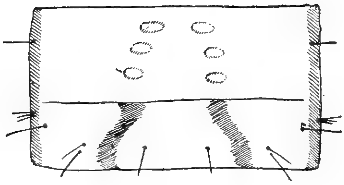
506, *Tipula oropezoides*; 507, *T. nobilis*; 508, *T. caloptera*; 509, *T. dejecta*; 510, *T. usitata*; 511, *T. ignobilis*; 512, *T. iroquois* (supposition)



TIPULA OROPEZOIDES, LARVA

513, Mentum; 514, hypopharynx; 515, mandible; 516, fifth abdominal segment, dorsal aspect; 517, fifth abdominal segment, ventral aspect; 518, spiracular disk

520



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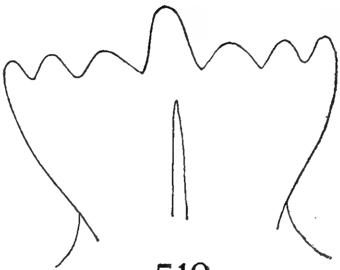

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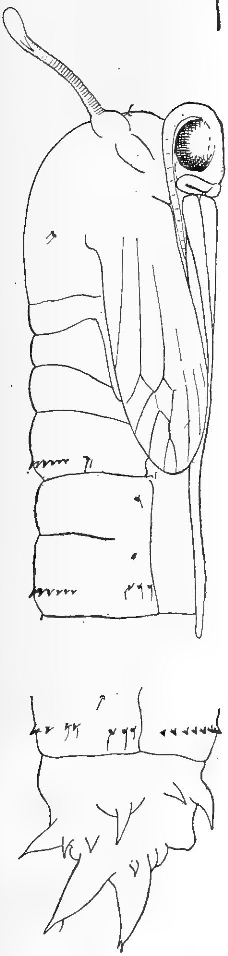

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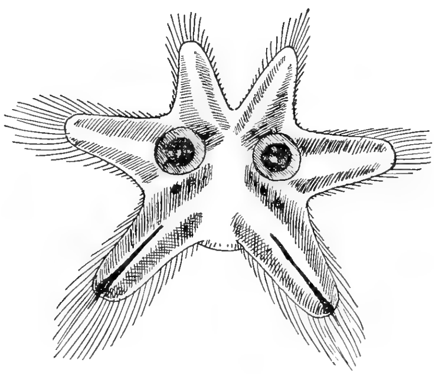
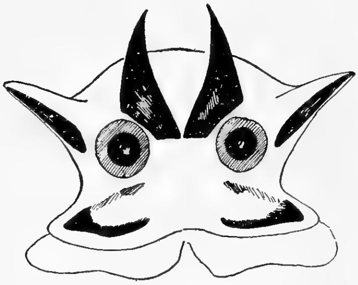


522

TIPULA COLLARIS

Larva: 519, mentum; 520, hypopharynx; 521, fifth abdominal segment, dorsal aspect; 522, spiracular disk

Pupa: 523, male, lateral aspect



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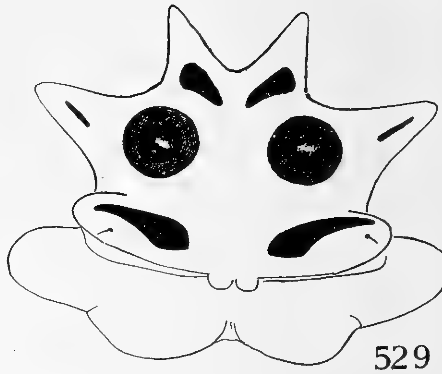

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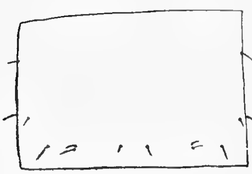

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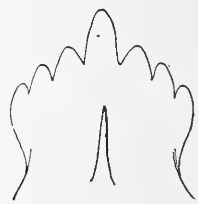

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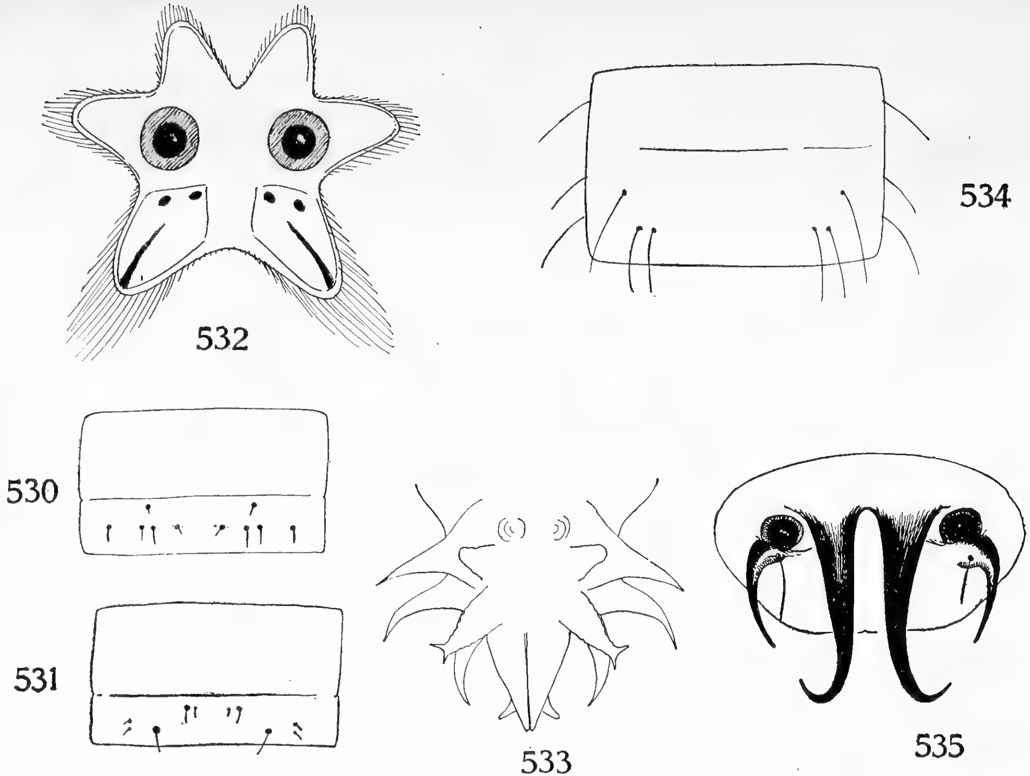
TIPULA DEJECTA, T. USITATA, AND T. TRIVITTATA

Tipula dejecta, larva: 524, mentum; 525, hypopharynx; 526, spiracular disk
Tipula usitata, larva: 527, fifth abdominal segment, dorsal aspect; 528, spiracular disk
Tipula trivittata, larva: 529, spiracular disk

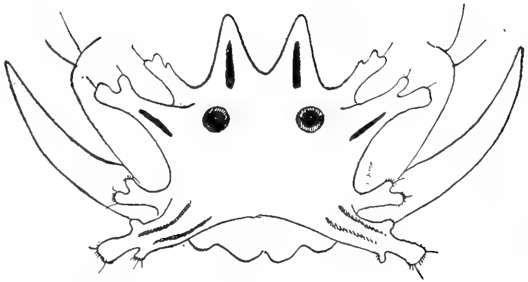


TIPULA IGNOBILIS AND TIPULINE NO. 2

Tipula ignobilis, larva: 530, fifth abdominal segment, dorsal aspect; 531, fifth abdominal segment, ventral aspect; 532, spiracular disk

Tipula ignobilis, pupa: 533, female cauda, dorsal aspect

Tipuline No. 2, larva: 534, fifth abdominal segment, dorsal aspect; 535, spiracular disk



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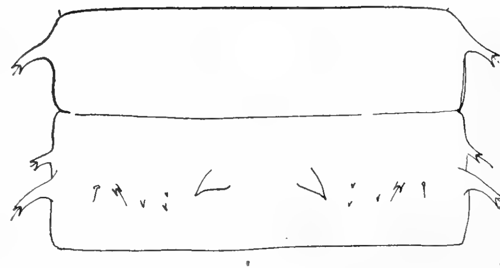

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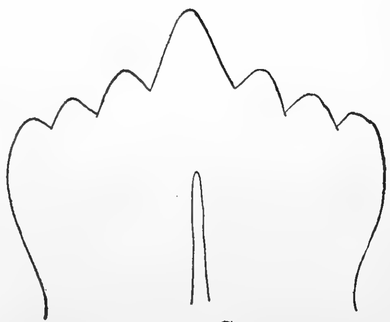

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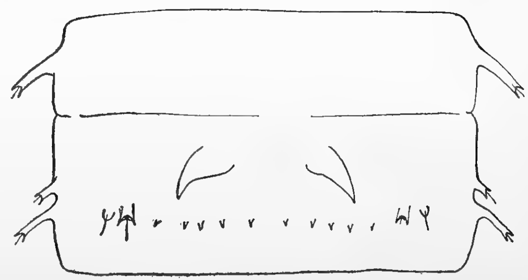

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TIPULA ABDOMINALIS

Larva: 536, mentum; 537, spiracular disk
Pupa: 538, fifth abdominal tergite; 539, fifth abdominal sternite

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(When more than one page reference is given, the more important references are italicized)

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